Lizards at elevation: thermal ecology and emergence activity of alpine lizards in Otago

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Abstract

The alpine zone is a rugged habitat that is difficult for any species to inhabit year-round. Many that do so are large mammals with specific behavioural or physiological adaptations that enhance survival in these high-elevation and often very cold environments. Lizards also inhabit this zone, but their ectothermic nature makes them especially vulnerable to the extreme temperatures and long winters. New Zealand has a number of poorly known alpine lizards in Otago, including the orange-spotted gecko (*Mokopirirakau* 'Roy's Peak') and multiple species of *Oligosoma* skinks. The orange-spotted gecko is a newly discovered species that is only known from the alpine zone whereas *Oligosoma* skinks can be found at lower elevations. Little is known about how these lizards survive in their alpine habitat. As a result, they provide a valuable opportunity to increase our understanding of the thermal ecology of lizards living in cold environments. Information gained through studying these species can increase our ability to manage alpine lizards and improve our understanding of threats to animals living in this zone. Therefore, the aims of this thesis were to investigate the thermal ecology of these lizards, especially the orange-spotted gecko, in order to understand what temperatures, they are exposed to and how these ectotherms interact with their environment in the alpine zone.

I first examined available temperatures in the alpine zone. Data loggers were placed in likely lizard microhabitats over the active season of October 2018-March 2019. These loggers recorded a wide range of temperatures including temperatures below 0°C and in excess of 50°C. I also compared daytime skin temperatures of orange-spotted with temperatures of the underside of their occupied rock to understand how lizards were thermoregulating and how this behaviour differed with reproductive status and across the active season. Reproductive females maintained higher skin temperatures than adjacent rock temperatures when the rocks were below 20° C but maintained lower body temperatures than those of their occupied rock when the rocks surpassed 25°C. When compared to other adult geckos (males and non-reproductive females), reproductive females maintained higher daytime skin temperatures, suggesting that they use the available microhabitats differently. Skin temperatures of non-reproductive females and males had a more linear relationship with rock temperatures.

I also monitored the emergence behaviour of lizards to increase our understanding of activity periods and how emergence is influenced by environmental conditions. To monitor emergence, trail cameras were left in the field. Sightings of geckos and skinks were compared with temperatures gathered by the microhabitat dataloggers and with other weather variables (presence of rain, snow, and the strength of wind). I obtained evidence of the orange-spotted gecko (potentially pregnant females) openly basking during the day, which is otherwise undocumented for this nocturnally foraging gecko. I further found that strong winds negatively influenced the presence of geckos on camera at night. During the day, warm surface temperatures increase gecko presence, while presence of rain and strong winds greatly decreased sightings. Skinks were only seen by day, and presence was directly related to surface temperatures whereby more skinks were found on warm days and observations of skinks dropped dramatically when poor weather (wind and rain) were present. Lastly, I confirmed the presence of several introduced mammal species (including cats and stoats, which are known predators of lizards) in this alpine habitat.

My study has provided an indication of what combination of time of day, temperature, and other weather variables create the optimal environment for orange-spotted gecko activity. We can use this information to inform monitoring programs so that the latter are conducted during optimal weather windows to increase the chances of observing lizards. With a strong monitoring programme, we can learn about threats these species face whether they be anthropogenic or from predators. Finally, knowledge gained through well informed monitoring programmes will promote effective management of alpine lizards in the future.

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Chapter 1 General introduction

The world's mountain regions contain steep slopes, high peaks, massive valleys and foothills, which are home to an impressive number of vertebrate species. For example, mountainous regions host around 85% of the world's species of amphibians, mammals and birds while consisting of only 25% of the terrestrial land mass (Rahbek et al. 2019). Within mountains exists the alpine zone, a high-elevation area above the treeline with extended periods of snow, rocky fields, and continuous to scattered tundra vegetation (Love 1970). Alpine ecosystems cover only 3% of the world's land area and their biomass is low compared to other ecosystems like shrublands or woodlands (Hecnar and M'Closkey 1998, Körner 1995; Rundel and Millar 2016). The most defining characteristic of the alpine zone is its climate. These regions are characterised by low mean temperatures, large variation in daily temperatures, low effective moisture, high winds, long periods of snow cover, and intense sun exposure (Billings and Mooney 1968; Martin 2001).

Not surprisingly, the species that inhabit the alpine zone have developed specialised strategies to cope with the harsh environment. These adaptations vary from avoidance tactics, like hibernation, which is observed in small alpine mammals like marmots (*Marmota marmota*; Arnold 1988; Tafani et al. 2012) to biological responses, such as flexible reproductive timing to cope with the seasonality of resources, as observed in many alpine arthropods (Sømme 1989). Other species of invertebrates such as the New Zealand wētā (*Hemideina maori*) have evolved biological responses, such as freeze tolerance, which allows individuals to freeze and thaw in tandem with their environment without suffering any ill effects (Ramløv 1999). As a result of cold adaptations, geographic isolation, and glaciation the alpine zone has a high degree of taxonomic richness, speciation, and endemism (Meyer and Thaler 1995). In New Zealand for example, floral diversity in the alpine zone is quite high with over 600 species of vascular plants, the majority of which (~92%) are endemic (O'Donnell et al. 2017).

1.1 Alpine ectotherms

When compared to alpine endotherms, which often have thick pelage or plumage to insulate them against cold alpine weather, alpine ectotherms are especially influenced by environmental pressures in the alpine zone (Martin 2001). For ectotherms, environmental temperature determines body temperature because ectotherms do not generate enough metabolic heat, nor do they have sufficient insulation, to raise and keep body temperature high by metabolic means (Brown and Au 2009). Instead, ectotherms rely on external heat sources to reach and maintain preferred body temperatures at which physiological and biochemical processes, such as digestion and locomotion, are optimal (Zamora-Camacho et al. 2016). This makes living in the alpine zone exceptionally challenging for ectotherms because the alpine environment reaches both low and high temperature extremes and winters often last longer when compared to lower elevations (Billings and Mooney 1968). As a result, alpine ectotherms will often experience wide fluctuations in body temperature in a single day, coupled with longer periods of cold temperatures, making it difficult for individuals to remain at their preferred body temperature (Kern et al. 2015).

To reduce the impact that continuous, reoccurring, or sudden changes in temperatures have on their system, ectotherms rely on behavioural ways of keep their body temperatures within a preferred range for as long as possible (Angilletta 2009; Bouazza et al. 2016). For example, alpine butterflies (*Colias meadii*) use different body postures to manage their exposure to the sun, allowing them to heat up or cool down as necessary (Buckley and Kingsolver 2012). When individuals are too cold, they close their wings and face their ventral, hindwing surfaces perpendicular to the sun. When they are too warm, they change posture so that their closed wings are parallel to the sun, reducing the surface area of their wings that is exposed to the sun (Buckley and Kingsolver 2012). High-elevation grasshoppers (*Trimerotropis suffsa*) use similar tactics in that they position themselves so that their bodies are perpendicular to the sun's rays in order to absorb additional heat (Gillis and Possai 1983). However, these strategies can be quite costly as active surface thermoregulation can increase predation risk, and the time spent regulating one's body temperature could be spent in other activities, such

as foraging (Verwaijen and Van Damme 2007) or reproducing (Huey and Slatkin 1976; Zamora-Camacho et al. 2016).

A particularly intriguing group of alpine ectotherms that face these challenges are alpine squamates (lizards and snakes). Despite mountainous regions not being particularly hospitable for ectotherms, there are examples around the world of squamates living at high elevations in extreme environments. These include the Atlas day gecko (*Quedenfeldtia trachyblepharus*) which lives in the mountain range of the High Atlas in Morocco at elevations of 1400 to 4000 m above sea level (a.s.l.; Comas et al. 2014) and the Iberian rock lizard (*Iberolacerta cyreni*) which has a restricted distribution in alpine habitats ranging from 1600 and 2590 m a.s.l. in several mountain ranges in central Spain (Monasterio et al. 2009). Other examples include the alpine she-oak skink (*Cyclodomorphus praealtus*), the Guthega skink (*Liopholis guthega*), and the grassland tussock skink (*Pseudemoia pagenstecheri*) which are found in mountain regions of Australia above 1500 m a.s.l. (Sato et al. 2014). Although the majority of squamates found exclusively at high elevations are lizards, snakes can also be found in the alpine zone. An example is the asp viper (*Vipera aspis*), which is found throughout central Europe at elevations of up to 2000 m a.s.l., though it does not exclusively live in the alpine zone (Broennimann et al. 2014).

Internationally, studies that focus on the thermal ecology of alpine squamates often examine how body temperature relates to environmental temperatures and refuge use (Martín and López 1999; Ibargüengoytía 2005; Aguilar and Cruz 2010; Zamora-Camacho et al. 2016). In these studies, individual field body temperatures (T_b) are recorded by measuring skin or cloacal temperature immediately after an individual is captured (Kearney and Porter 2004; Monasterio et al. 2009). Field body temperatures can then be compared with the selected temperature of individuals (T_{sel}), which is the mean of temperature selected by squamates in a controlled laboratory thermal gradient with no thermoregulatory restrictions (Kearney and Porter 2004). Field body temperatures can also be compared with environmental or microhabitat temperatures, which are often used to determine the quality of the thermal environment (Zamora-Camacho et al. 2016). Understanding how T_b differs from T_{sel} gives researchers an idea of how limiting the environment is for a specific squamate. For example, for many alpine

squamates, T_b is often below their $T_{sel,}$ which implies that the thermal quality of their environment is limiting the body temperature of these animals (Aguado and Braña 2014). Comparing the relationship of T_b to environmental temperatures helps us understand how effectively a squamate is thermoregulating as well as which environmental factors are limiting the species from reaching their T_{sel} (Aguado and Braña 2014).

Another relevant topic of study is activity periods, or the times of day or night that a lizard is active on the surface. Activity periods influence what threats a species is exposed to and what temperature or other weather variables they experience (Melville and Swain 1997; Martín et al. 2009). Squamates are active within a range of temperatures that allow them to reach high body temperatures that promote locomotion (Angilletta 2009). Studies on this topic span from those delivering a broad understanding of when squamate activity periods take place, how they have evolved and how they are influenced by temperature or other weather variables (Melville and Swain 1997; Meiri et al. 2013) to those delivering a more intricate understanding of the relative costs and benefits of thermoregulation and how individuals balance thermoregulating with predation risks or other activities such as foraging or reproducing (Martín and López 1999; Martín et al. 2003). For example, in a controlled experiment the common wall lizard (*Podarcis muralisI)* preferred warm retreats and actively avoided “unsafe” retreats containing chemical cues of a common predator, a saurophagous snake (Amo et al. 2004). When made to choose between a warm but unsafe retreat, and a safe but cold retreat, the lizards chose the safe but cold retreat. In the wild, avoiding predators through the use of cold retreats could have major fitness implications such as a reduced ability to catch prey as squamates spend more time basking (to make up for cold temperatures in their retreats) or cause them to forage at suboptimal temperatures with a lower sprint speed (Amo et al. 2004).

1.2 New Zealand’s alpine lizards

The alpine zone in New Zealand is significant, covering 11% of the total land area (O’Donnell et al. 2017). After geologically recent tectonic activity and glaciation events, phylogenetic branching of birds, invertebrates, plants, and lizards has occurred quite

extensively in the alpine zone (Wallis and Trewick 2009; Knox et al. 2019). Consequently, the New Zealand alpine zone is noteworthy because of its relatively high species richness of lizards. New Zealand has 110 species of recognised lizard taxa (including undescribed species) of which seven are Data Deficient, 37 are Threatened (Nationally Critical, Nationally Endangered and Nationally Vulnerable combined) and 52 are At Risk (Hitchmough et al. 2016). Of those species, there are at least 13 gecko and 17 skink taxa found within the alpine zone with seven that are restricted to and nine that primarily use alpine habitat (O'Donnell et al. 2017; Knox et al. 2019). For geckos, in particular, this is especially impressive when put at a global context. There are around 1553 gecko species worldwide, most of which are found in warm habitats (Carranza and Arnold 2006; Uetz 2010; Gamble et al. 2015). As a result, the existence of 13 proposed species of geckos within the alpine zone in a relatively small country such as New Zealand is remarkable.

In addition to their prevalence in the alpine zone, New Zealand geckos have a number of other traits that are uncommon for geckos. Firstly, New Zealand geckos are all viviparous (live-bearing) rather than oviparous (egg-laying). Although viviparity has evolved over 100 times among the 10671 or so species of squamates, it is a trait that has rarely evolved in geckos. Worldwide, viviparous geckos are found only in New Zealand plus two species in New Caledonia (Guillette 1993; Girling et al. 1997; Sites et al. 2011). Viviparity is an important cold-climate adaptation in lizards as giving birth to live young allows pregnant females to manipulate the thermal environment experienced by their embryos for their entire development period, allowing the mother to maximise the fitness of her offspring (Shine 2014). As a result, pregnant female geckos often select warmer body temperatures than non-pregnant females and males by devoting more time to basking (Cree and Hare 2016a). This leads to another uncommon feature of New Zealand geckos, which is that some are active during the day, like the diurnal, cryptic, green gecko (genus *Naultinus*; Whitaker 1987; Hare et al. 2007). Geckos are the only lizard clade that consists mostly of nocturnal species; 75% of the 1553 described species are nocturnally active (Gamble et al. 2015). As a result, geckos have many adaptations to low light and low temperatures suggesting that nocturnality evolved early in their evolution (Gamble et al. 2015). In New Zealand, however, there is extensive evidence of diurnal activity in many

species of geckos. Furthermore, some New Zealand geckos that are classified as nocturnal have been observed openly basking and foraging during the day (Jewell 2008; Romijn et al. 2013; Gibson et al. 2015). As a result, the study of alpine geckos provides a valuable opportunity to improve our understanding of a group of squamates whose members do not follow the common characteristics of their group.

Skinks in New Zealand are a part of the Eugongylinae sub-family, and include at least 61 species within the single genus *Oligosoma* (Chapple et al. 2016). New Zealand skinks show multiple cold-weather adaptations, like viviparity, a 'left-shifted' performance curve, along with a low T_b and T_{sel} when compared with skinks from other countries (Hare et al. 2016). Like As with geckos in New Zealand, the activity periods of New Zealand skinks are not well defined. Half of the nocturnally described species have also been observed foraging during the day, while some diurnal species are known to be also active at night (Hare et al. 2016). Despite the existence of at least 17 species of skinks in New Zealand that enter the alpine zone, there is little information on the activity periods or thermal ecology for these species. Recent studies have instead focussed on species descriptions for newly discovered species including Oligosoma pikitanga and *Oligosoma judgei* (Bell et al. 2008; Patterson et al. 2009), and have also explored the phylogeography of a few species (O'Neill et al. 2008). As a result understanding remains limited about the activity periods and thermal ecology of skinks in the alpine zone.

1.3 Study species and site characteristics

Among geckos, a newly discovered species in the New Zealand alpine zone is the orange-spotted gecko (*Mokopirirakau* sp. “Roys Peak”; Fig. 1.1). The orange-spotted gecko is

Figure 1.1 A posed orange-spotted gecko (*Mokopirirakau* sp. “Roys Peak”) in its alpine habitat. Photo: Aaron Bertoia.

known to exist on the mountain ranges in central Otago with a large population on the Crown Range (Knox 2017). It has a snout-to-vent length (SVL) that ranges from 43 to 90 mm with a mean of 73 mm and usually weighs between 9–15 g (Knox et al. 2019). This species can be found above the tree line between 1100- 1620m a.s.l. and its threat status is Nationally Vulnerable (Hitchmough et al. 2016). Few studies have been conducted on this species because individuals are fairly cryptic and live in remote, hard-to-reach areas (Knox et al. 2019). Past work has attempted to increase our general knowledge of distribution, population density and demographics. However, little is known about their general biology, including thermal biology, and reproductive frequency (Knox et al. 2019).

Several species of *Oligosoma* skinks occur in the same habitat as the orange-spotted geckos. The majority (~95%) of individual skinks are likely to be McCann's skink (*O. maccanni*); however, the Canterbury grass skink (*Oligosoma* aff. *polychroma* Clade 4) and the Lakes skink (*Oligosoma* aff. *chloronoton* ‘West Otago’) and are also known to be present (the McCann’s

skink and Canterbury grass skinks are listed as not threatened while the Lakes skink is Nationally Vulnerable). These species are understudied and as a result, we know little about the activity periods of these skinks. Although skinks were not the primary focus of my thesis, their inclusion provided a good opportunity to increase our overall understanding of alpine squamates.

Poaching of New Zealand lizards has become a significant threat to some species and populations throughout New Zealand (Knox and Monks 2014; Lettink and Hare 2016). To help reduce the poaching risk for orange-spotted geckos at my field site I have withheld the exact location and refer to it as QL-A, as used by Knox et al. (2019). GPS points, and photos containing any telling geography, have also been excluded from this thesis. QL-A comprises exposed rock on the steep upper slopes of a mountain with elevations ranging from 1000 to 1650 m a.s.l. The habitat consists of scree slopes, with some rocky bluffs, and aggregations of loose surface rocks. There is a walking trail that takes trampers and mountain-bikers directly through a portion of the habitat, but this trail did not go through the parts of the habitat that were studied in this thesis. Nonetheless, there is some potential interaction between recreational users and the gecko habitat, but it is relatively light when compared to more popular tracks throughout New Zealand. Weather in the summer is quite variable; air temperatures can reach in excess of 30°C during the day but can also fall below 0°C at night (pers. obs.). Summer conditions are relatively hot, dry and windy with periods of intermittent rain. During the winter the site is snow-covered for 3- 4 months a year, but early snowfalls in April or late snow in October/November are also frequent.

1.4 Aims and objectives

My research is affiliated with, and makes a major contribution to, the Department of Conservation's alpine research programme. The goal of this programme is to develop effective tools for managing threatened alpine ecosystems and species. A major focus of the programme is reviewing the threats to native alpine fauna (O'Donnell et al. 2017). This has been furthered through the development of a network of baseline monitoring sites to address drivers of predator dynamics in the alpine zone and a detailed study of effects of predators on rock wrens

(*Xenicus gilviventris*), the only bird endemic to New Zealand's alpine zone (Weston et al. 2018). Knowledge of alpine lizards and invertebrates is limited. As mentioned earlier, basic ecological information on orange-spotted geckos was reported by Knox et al. (2019). My study builds on this descriptive study by increasing our knowledge of the thermal ecology and emergence behaviour of the orange-spotted gecko and a group of *Oligosoma* skinks. As a result, it contributes directly to questions about how best to monitor alpine squamates, so that we can learn about the threats that affect these species and manage them appropriately.

The overarching goal of my research is to improve our understanding of the thermal ecology of alpine lizards in New Zealand, especially the orange-spotted gecko. Alpine lizards in New Zealand have no studies to date on their thermal ecology and information on the temperatures available in alpine habitats is limited. With the findings of this thesis I hope to provide insight into monitoring alpine lizards so that we can better understand the population dynamics and eventually be able to measure the impact of predator control and habitat protection strategies. The aims of this research will be addressed by asking the following questions:

1. What temperatures are available in the microhabitats of alpine lizards at QL-A?

   I address this question as part of Chapter 2. Temperature dataloggers were inserted in likely gecko microhabitats to record the temperatures that are available throughout the spring and summer. In Chapter 3 these data were compared with photographic evidence of emergence activity, of both geckos and skinks, to understand at what temperatures these squamates are active in their alpine habitat.

2. What field body temperatures are reached by orange-spotted geckos by day? And how do they vary among reproductive conditions? Do these body temperatures differ from those of gecko species found at lower elevations?

   These questions are addressed in Chapter 2. Using a mini infrared thermometer, I measured skin temperatures of adult orange-spotted geckos and microhabitat temperatures of the surface rock under which individuals were found. I made comparisons of skin temperature with surface rock temperature for reproductive

females, males and non-reproductive females to understand the relationship between gecko skin temperature and microhabitat temperature and how it is influenced by reproductive status.

3. What are the activity periods of lizards, both orange-spotted geckos and *Oligosoma* skinks, in this alpine environment and how does that behaviour relate to environmental temperatures and other weather conditions?

   These questions will be addressed in Chapter 3. I used trail cameras to monitor both daytime and night-time emergence activities of these lizards to see if these species are nocturnally or diurnally active (or a mixture of the two). Emergence activity was compared with microhabitat temperature and other weather variables to increase our understanding of what conditions promote or inhibit activity in this alpine environment.

4. What are the selected temperatures of orange-spotted geckos?
   I attempted to develop, with assistance, and to test a new portable thermal gradient for measuring the thermal preference of lizards in the field without access to electricity mains. However, despite many attempts and refinements it was ultimately unsuccessful at maintaining an appropriate and stable range of substrate temperatures in the field. This aspect of the work is described in Appendix 1.
5. Effective monitoring tools for squamates are based on strong knowledge of a species' thermal biology and activity patterns. Species- specific knowledge is critical for understanding population trends and how they respond to management strategies. As a result I want to know how can the information gathered in this thesis inform management to help generate a species-specific management plan for alpine geckos and skinks? This question is initially addressed in Chapters 2 and 3 and is more deeply discussed in Chapter 4.

Chapter 2 Orange-spotted geckos (*Mokopirirakau* sp. "Roys Peak") achieve similar maximum body temperatures to lower-elevation geckos despite their alpine environment

2.1 Introduction

An ectotherm's body temperature influences an array of physical processes, including locomotion, reproductive physiology, and metabolism (Angilletta 2009; Christian et al. 2016). Thus, the ability to stay within a preferred range of temperature has ecological consequences such as being able to escape from a predator, catch prey, reproduce, and develop (Christian et al. 2016). As a result, most ectotherms try to regulate their body temperature through behavioural means in an attempt to stay within an acceptable temperature range (Angilletta 2009). However, reliably regulating one's body temperature is not always easy for ectotherms as ambient temperatures in the environment vary over space and time. One region with a notoriously variable temperature range is the alpine zone. This region experiences large temperature swings, prolonged winters, strong seasonality of resources and high thermal constraints (Billings and Mooney 1968; Martin 2001). As a result, this environment is not the most hospitable environment for ectotherms.

None-the-less, lizards have been found to occupy alpine zones in several parts of the world including Europe and South America. For example, Cyren's Rock Lizard (*Iberolacerta cyreni)* a diurnal oviparous lizard inhabits elevations between 1700 and 2350 m above sea level (a.s.l) in central Spain (Aguado and Braña 2014). This lizard makes behavioural adjustments to suit changes in its thermal environment, including changes in daily activity patterns, selection of microsites, orientation to the sun, and posture modifications. These adjustments allow the lizards to attain a body temperature that is close to the preferred range during daylight hours even when environmental temperatures surpass both the upper and lower limits of their preferred temperature range in a single day (Aguado and Braña 2014). Even with these adaptations, the Cyren's Rock Lizard often experiences field body temperatures that are lower than their preferred temperatures. This highlights that even with behavioural adaptations,

lizards in cold alpine environments are often constrained from reaching their preferred temperature.

In South America, *Liolaemus pictus argentinus*, a diurnal, viviparous lizard found up to 1600 m a.s.l in the Patagonian Andes of Argentina, uses specialised retreats to avoid sub-zero temperatures (Cecchetto et al. 2019). Even in winter, when air temperatures fall below 0°C, these lizards have access to retreats that rarely reach temperatures that below freezing. Interestingly, during spring and autumn, high-elevation refuges experience more days above 5°C than lower-elevation retreats in forested areas as the forest vegetation cools down the soil surface through direct shading and, indirectly, through evapotranspiration. As a result, lizards that choose to reside in higher-elevation refuges have more access to days above the critical thermal minimum, the temperature at which an individual is so cold that it loses motor function, of the species allowing them to partake in activities such as foraging, or moving to another refuge (Cecchetto et al. 2019). This study helps show that even though temperatures in alpine environments can be extreme, lizards do have access to different microhabitats that provide mild conditions throughout winter.

New Zealand is a fascinating location to study the thermal ecology of cool climate lizards (Cree and Hare 2016a). This is because many small, nocturnally foraging, lizards occur even in southern New Zealand (latitude > 44°S), and several can be found primarily or exclusively above the climatic tree line in the alpine zone (above ~1000 m a.s.l.; Hare et al. 2016). However, to date, detailed studies are limited to the mid-elevation near-coastal population of the Otago/Southland or korero gecko (*Woodworthia* 'Otago/ Southland') at Macraes in eastern Otago. As a result of living in a cool climate, korero geckos have developed multiple adaptations that allow them to survive. For example, pregnant females often maintain a higher body temperature than non-pregnant females and males and this promotes the development of their young during pregnancy (Rock et al. 2000; Cree and Hare 2016b). High body temperatures are attained by thermoregulating via postural adjustments under rocks, in addition to open and partial basking during the day, despite their official nocturnal classification (Gibson et al. 2015). Additionally, pregnant females in this population are able to hold full-term embryos *in utero*

over winter delaying birth until spring when the environment is warm, an impressive cold-climate adaptation (Cree and Hare 2016a).

Compared to the korero gecko, much less is known about the lizards that occupy the alpine zone, a large region that covers 11% of the land area (O'Donnell et al. 2017; Knox et al. 2019). At least 13 gecko species extend into the alpine zone in New Zealand, one of which is the recently discovered (1998) orange-spotted gecko (*Mokopirirakau* "Roys Peak"). This cryptic, nocturnally foraging gecko is confined to the high alpine regions of western and central Otago, with a latitude of -44° S and an elevation between 1150–1620 m a.s.l. This species currently has a threat ranking of 'Nationally Vulnerable'. It is considered to be sparsely distributed, data poor, and have a restricted range (Hitchmough et al. 2016; Knox et al. 2019). Only one published study on this species exists, which is a collation of exploratory surveys to increase general knowledge of the species (Knox et al. 2019). Through these surveys, we know of one large population, in which 95 geckos were found. When examined, female geckos showed a wide range of reproductive conditions suggesting that pregnancies may take two or more years. Lastly, these surveys show us that orange-spotted geckos occupy scree slopes, rock jumbles and boulder fields.

In this chapter, I aim to improve our understanding of the thermal ecology of the orange-spotted gecko. To achieve this, I first recorded environmental temperatures with dataloggers that I placed in microhabitat locations where geckos are likely to be found based on actual observations of geckos using the habitat. Second, I captured geckos by rock turning during the day to record their "spot" skin temperature as well as the temperatures of the retreat that each gecko had occupied. Finally, I used a newly miniaturised bio-logger developed for use on New Zealand lizards (Virens and Cree 2018) to monitor the skin temperature of free-roaming geckos continuously. With these data, I attempted to answer several questions: (1) What temperatures are available in the microhabitats of orange-spotted geckos? (2) How does the skin temperature of orange-spotted geckos relate to the temperature of rocks above their retreat-site? Does that relationship change with reproductive status or season? Lowland New Zealand geckos maintain higher skin temperatures on fine sunny days than non-pregnant females and males. As a result, I expect orange-spotted geckos to do the same. (3) What do

continuous records of skin temperature tell us about lizard activity and probable temperature preference in the alpine zone? I expected skin temperatures (as measured by the miniaturised bio-logger) to show evidence of active thermoregulation during the day, via quick changes in body temperature, as many New Zealand geckos actively thermoregulate diurnally, despite their nocturnal classification (see section 2.2.3.).

2.2 Materials and methods

2.2.1 Field site

Gecko surveys took place in a specified location within the Queenstown lake district. Due to the high potential for the illegal collection of this animal for the pet trade, I have avoided making any references to exact locations. Instead, I refer to the field site as QL-A, the same system used by Knox et al. (2019). The site is comprised of exposed rock on the steep upper slopes of a mountain with altitudes ranging from 1000 to 1650 m a.s.l. The habitat mainly consisted of scree slopes, with some rocky bluffs, and aggregations of loose surface rocks. Usually, the field site is snow-covered for 3-4 months a year, but early snowfalls in April or late snow in October/November are also frequent. The dominant vegetation is narrow-leaved snow tussock (*Chionochloa rigida*) and other species of shrubs and grass such as dracophyllum (*Dracophyllum rosmarinifolium*) and common speargrass (*Aciphylla squarrosa*) are also present (Figure 2.1; Knox et al. 2019).

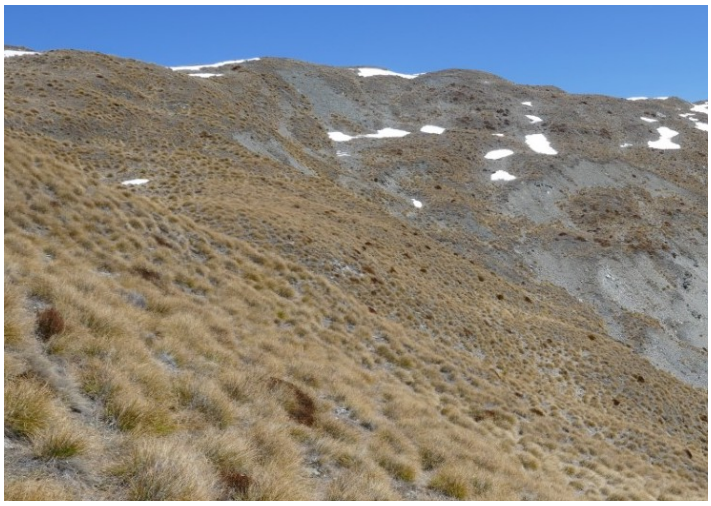

Figure 2.1 Example of orange-spotted gecko habitat during summer. Photo by Alison Cree.

2.2.2 Temperatures of available microhabitats across a calendar year

I used Thermochron iButton data loggers (Maxim Integrated, San Jose, CA, USA) to record ambient temperature in four potential gecko microhabitats. The devices recorded from 21 October 2018 until 29 March 2019. I left another set of devices to record over winter, but I was not able to retrieve them for inclusion in the thesis. All devices were programmed to sample every hour on the hour at a resolution of 0.5°C. I selected five total locations (replicates) for each set of four microhabitats. The five locations were chosen based on where I found pregnant females during my first gecko survey in October 2018.

The first microhabitat position is the “bottom rock” position (note that locations are named with reference to a gecko within the retreat). To monitor this position a data logger was placed on the substrate (which is usually an underlying rock) beneath a surface rock, in the retreat where a pregnant female was found. This microhabitat represents a gecko that is pressing itself against the ground within its rock retreat. The second microhabitat position is the “top rock” position, which is simulating a gecko that has pushed itself against a surface rock for warmth. To monitor this position, I attached a data-logger to the underside of the same surface rock that covered the bottom rock logger. The third microhabitat position is the “deep crevice” position. To monitor this position, I placed a data-logger at least 20-40 cm into the closest available crevice, though the actual depth varied by location as some crevices were more accessible than others. This position simulates an area where I predicted a gecko might go in poor weather conditions, including over winter. The final microhabitat position is the “copper

model" position. Copper models are standard tools used to simulate temperatures that would be experienced by lizards if they were basking at that position in the wild (Gibson et al. 2015; Penniket and Cree 2015)**.** Each copper model consisted of a sealed, hollow 24 mm diameter copper pipe that was 110 mm long. Copper models have been shown to reach comparable temperatures to freshly euthanised korero geckos when exposed to radiation from a heat lamp (Gibson et al. 2015). At the time of placement, I did not know whether orange-spotted geckos openly basked during the day, so I placed the copper model in a potential basking position.

First, all data-loggers were programmed with a time delay so that they would start recording once they were attached to their microhabitat location. To help weatherproof the devices, I wrapped them in 2 x 2 cm squares of parafilm, a flexible self-sealing thermoplastic (Bemis Company, Inc, Neenah, WI United States). For the top and bottom rock positions, the devices were then glued directly onto the rock using "THE ONE", an all-surface adhesive (Selleys, New Zealand). For the top rock location, the logger was glued to the underside of the top surface rock. For the bottom rock location, the logger was glued to the top of the substrate underneath the surface rock. The substrate usually was another rock that lay beneath the surface rock layer. Once the adhesive was dry, I taped over the devices with Scotch duct tape to provide another layer of weather protection.

For the loggers in deep crevices, I first tied a long string of dental floss around the logger. The logger was then weatherproofed with parafilm and wrapped in duct tape allowing the long string of floss to trail outside of the tape. I then placed the dataloggers into the crevice by hand. Finally, I secured the end of the floss to the entrance of the crevice either by tying it to a nearby plant or taping it to the rocks that form the crevice. The floss acted as a retrieval device for the deep-crevice loggers. When I relocated the loggers, I pulled on the floss to retrieve the data logger from the crevice.

To prepare the loggers for insertion in to the copper model, I first inserted the data loggers into a plastic holder that allowed the datalogger to not directly touch the copper model itself, thereby recording the air temperature inside the model instead of measuring the temperature of the copper. After I placed the logger and its holder into the copper model, I then sealed the models by crimping the open end of the model together and filling the opening

with an epoxy glue. Copper models were then painted a light brown colour to match the colouration of many orange-spotted geckos. I then secured the copper models to the top of the chosen rock using a small amount of “THE ONE” adhesive. Models were oriented north to south for consistency (Figure 2.2).

Figure 2.2 Examples of rocks on which I attached copper models to simulate basking lizards. Photo: Alison Cree

2.2.3 Gecko surveys

I conducted daytime searches for orange-spotted geckos between October 2018 and April 2019. Four surveys took place during this period, 10-28 October 2018, 22 November-3 December 2018, 20 January-1 February 2019 and 23 March-3 April 2019. During these surveys, searches for geckos took place between 10:00 to 17:00 h focusing on times when conditions were favourable for finding geckos (I.e. fine days between 10-22 °C air temperature with little or no wind). When the habitat was too cold, too hot, extremely windy, or when rain fell searches for geckos became less successful. As a result, I planned trips for favourable weather windows where multiple geckos could be caught to maximise time on the mountain.

During the surveys, I caught free-roaming geckos by turning large (approximately 30 by 40 cm), flattish surface rocks that were in favourable locations to absorb sunlight. If there were no geckos present under the rock, I would return it to the exact location and position where it was found. If I did find a gecko under the rock, I would endeavour to catch it by hand. When moving within the habitat I avoided loose scree slopes which would potentially put geckos and

searchers at risk. I also established consistent walking routes throughout surveys to reduce the impact that the study had on the habitat as a whole. When I found a rock that could provide adequate shelter to a gecko, it would be turned over by hand.

2.2.4 Spot body temperature and morphometrics

Spot body temperatures are one-time measurements of skin temperatures taken from lizards at capture. I used three compact mini-infrared thermometers (mini-IRT ; Digitech® model QM-7218, Jaycar, Rydalmere, NSW, Australia) to take all temperature measurements during surveys. Mini-IRTs are quick and easy to use and, when employed properly, have been shown to record temperatures that are comparable to those taken by a cloacal thermocouple on korero geckos (Chukwuka et al. 2019). These devices are also cheaper and have a longer battery life than other alternatives, such as an infrared camera (Chukwuka et al. 2019). The mini IRT was positioned within 5 mm of the dorsal posterior abdomen while not touching the gecko's skin directly (Chukwuka et al. 2019). The skin measurement was taken within 30 s of catching the gecko to minimise the effect that handling had on the gecko's body temperature. Directly after, I recorded the temperature of the underside of the surface rock that formed the top of the retreat (if viewed from the geckos perspective). This location is similar to where top rock loggers were placed. I recorded all temperature measurements within 1 min of finding the gecko.

To minimise the amount of time that I handled the geckos, I placed each gecko in a small cloth or canvas bag and stored them in a safe, shaded location until I was ready to proceed. In addition to skin temperature, I recorded snout-vent length (SVL), vent-tail length (VTL) and mass of the individual. The geckos would also be sexed when possible (sub-adults ≤ 58 mm are too small for sex to be identified), and all female geckos were palpated to try to estimate their stage of pregnancy. Palpation has proven to be an accurate technique for estimating the reproductive condition of small lizards such as New Zealand geckos (Wilson and Cree 2003). Following classifications from Knox et al. (2019) I initially classed reproductive condition as vitellogenic (firm, spherical structures in the mid-abdominal region), early-mid pregnant (softer, more oval structures, i.e. inferred conceptuses, along the sides of the

posterior abdomen), late pregnant (embryos with discernable form present) or non-reproductive (no detectable follicles or conceptuses). However, I did not have a method for independently verifying these stages and some distinctions can be subjective. Air temperature at the time of capture was also recorded with a Kestral 2500 digital weather meter (Nielsen–Kellerman, Boothwyn, PA, USA). Lastly, I took photos of the dorsal pattern of each gecko to aid in the development of a photo identification database curated by Carey Knox for DOC. When I finished processing a gecko, I returned it to the same retreat that I had found it in by encouraging it to return headfirst into the retreat.

In addition to the surveys that I completed from October 2018 to April 2019 I received data from Jo Monks (DOC) of a previous trip on 12 February 2017 that was conducted by the DOC alpine team. Those data include the spot body temperatures and morphometric measurements of seven adult orange-spotted geckos. These data were gathered using the same methods as described above.

2.2.5 Body temperatures from free-roaming geckos fitted with bio-loggers

I measured skin temperatures of a free-roaming gecko in the field for 24 h using a miniature bio-logger. The bio-logger weighed 0.34 g and is a miniaturised version of the Thermochron iButton. The iButton was reduced in weight and size by removing its steel housing along with any unessential components following the methods of Virens and Cree (2018). To aid with the recovery of the device I also attached a Pico pip VHF radio transmitter weighing a total of 0.29 g to the gecko (Pico Pip Ag 337 from Biotrack, Dorset, UK). The resulting attachments weighed a total of 0.62 g. As a result, I made sure only to select geckos that weighed more than 13 g so that the device did not weigh more than 5% of their total body weight.

I made four different attempts to obtain skin temperatures of free-roaming geckos. The first three attempts were unsuccessful as only one bio-logger was recovered. However, I found it months later in the scree by chance. An in-depth description of my unsuccessful attempts is available in Appendix 2. I was able to recapture one individual with my final attempt, which I will describe below.

First, the bio-logger was programmed to record gecko skin temperature every minute at a sensitivity of 0.5 °C using One Wire Viewer. When the logger was active, I placed a piece of double-sided Sellotape directly onto the bottom of the bio-logger. I then placed the bio-logger onto the dorsal side of the gecko posterior to its forelimbs. Next, surgical tape was put over the device to attach it to the skin more securely. I used Nexcare Micropore tape, which is a standard first-aid tape for human skin, as it has been used to attach transmitters to New Zealand geckos in previous studies (Hoare et al. 2007; Knox and Monks 2014). The Pico Pip transmitter was attached separately using the same methods, but the transmitter was placed just above the hind legs and oriented so that the transmitter antenna would follow the tail of the gecko (Figure 2.3). I began attempts to relocate the gecko from 24 h after attachment.

2.2.6 Statistical analysis

Chukwuka et al. (2019) found that the mini-IRTs became less reliable when measuring the temperature of individuals that were less than 5-7 mm wide as the thermometers picked up too much background heat. Since juveniles fell below this threshold, I removed them from the dataset. I then compared temperature readings made by the mini IRT with temperatures taken by a thermocouple inserted into the cloaca for 9 individuals (Alison Cree provided these data).

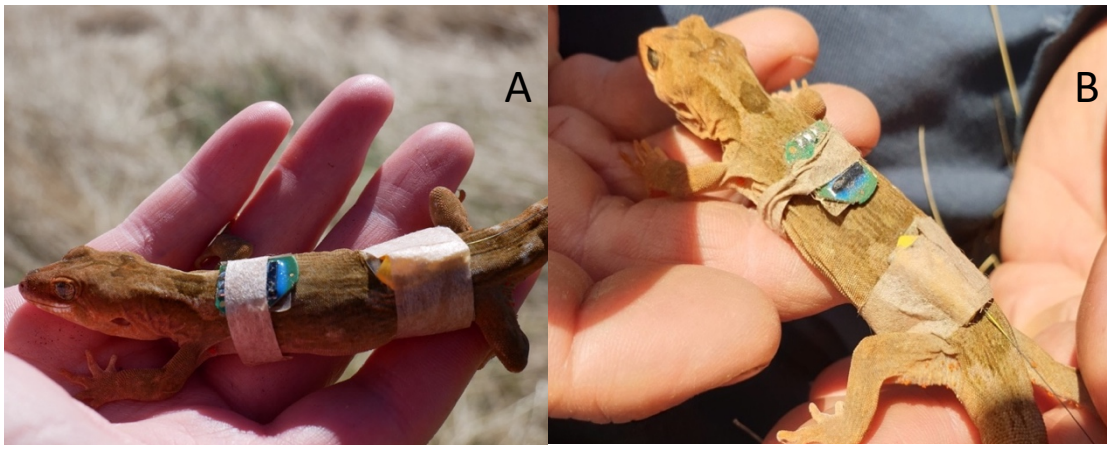

Figure 2.3 Photo of the successful bio-logger attachment method before the gecko was released (A) and after the gecko was relocated (B). The bio-logger is located just below the forelimbs while the VHF device is just above the hind limbs with the antenna following the tail.

Cloacal temperature is a common and reliable way to measure gecko body temperature, which is why it was used to confirm the validity of the IRT measurements (Weeks and Espinoza 2013; Tan and Schwanz 2015). A paired t-test showed no significant difference between

measurements from the IRT and from the cloacal thermocouple (P=0.586) and regression analysis on the same data showed a strong relationship between measurements from both devices (R^2= 0.842). The final data set included 73 orange-spotted geckos. The data set contained 49 females and 25 males, which consisted of 37 reproductive females (vitellogenic to late pregnant), and 36 non-reproductive females and males which I have grouped together as "other adults".

I completed all the analysis for this chapter in R (R Core Team 2018). First, I obtained mean hourly temperatures of the four microhabitats by averaging them across the five different locations (replicates) leaving one set of average hourly temperature recordings per microhabitat. I then compared all microhabitat positions graphically and with basic summary statistics.

I then compared the skin temperatures of males and non-pregnant females using a one-way ANOVA. There was no significant difference between the two groups ($F_{1,34}$ = 0.065, p = 0.88). These two groups also had very similar confidence intervals for the mean (μ= 19.4, 95% CI [16.1, 22.8] for females and μ= 19.0, 95% CI [17.1, 20.9] for males). As a result, males and non-pregnant females were grouped together to be compared against pregnant females in future analysis. The relationship between orange-spotted gecko skin temperature and the temperature of the top of the retreat was examined using a generalised additive model (GAM) generated by the MGCV package. I used the restricted maximum likelihood (REML) estimation to select smoothing parameters as it has been shown to perform better than the default generalised crossed validation (GCV) selection method which can under-smooth the shape of the relationship (Wood 2012). Skin temperature of the geckos was the response variable, with retreat top temperature and time of capture from sunrise, standardised by day length, as smoothed predictor variables. Season and reproductive status were also included as categorical variables. Season was split between spring, which consisted of October-December 2018, and summer, which consisted of January-March 2019.

I then separated the body and rock temperatures for reproductive females, and for other adults, into two separate models in order to see if the relationship between skin and rock temperature differed by reproductive status. These two new models shared the same format,

in which skin temperature was the response variable with the retreat top rock temperature and time of capture from sunrise as smoothed explanatory variables. Finally, I presented the temperatures recorded by the single bio-logger trace graphically. Unfortunately, I was unable to return to my field site in spring to retrieve overwinter data so at this stage I am unable to compare the body temperatures recorded from the bio-logger against microhabitat temperatures, although I expect to be able to do this eventually.

2.3 Results

2.3.1 Available microhabitat temperatures and thermal quality

The habitat that I studied contained a wide range of temperatures including some that were below 0°C even during the warmest months of the year. The copper model location showed the most substantial variance in temperature (Fig 2.4). The absolute maximum temperature recorded at the copper model position was 68.8°C while the absolute minimum was -6.5°C. This position recorded the highest mean maximum and mean minimum temperature across all four logger positions (Table 2.1). The top rock location was the next most variable location (Fig 2.4). Loggers at the top rock position recorded an absolute maximum of 52.0°C and an absolute minimum of -4.5°C. The bottom rock position was very similar to the top rock position (Fig 2.4; Table 2.1). Bottom rock data loggers recorded an absolute maximum of 52.0°C and an absolute minimum of -3.9°C. The most stable position was the deep crevice (Fig 2.4; Table 2.1). Deep crevice data loggers recorded an absolute maximum of 25.5°C and an absolute minimum of -1.5°C. Over a 24-hour period the copper model position heated up fastest and reached the highest temperatures. Top rock and bottom rock positions heated up more slowly and did not reach as high temperatures, but they maintained their heat longer into the evening than copper model positions. Deep crevice temperatures did not vary much throughout a single day (Fig 2.5).

Table 2.1 Mean absolute maximum and minimum, and annotated standard errors for microhabitat temperatures in spring and summer. Mean values are averages across the five loggers for each microhabitat position. Spring includes recordings from October-December 2019 and summer includes recordings from January-March 2019.

Microhabitat position	Maximum Spring (°C)	SE	Minimum Spring (°C)	SE	Maximum Summer (°C)	SE	Minimum Summer (°C)	SE
Copper model	54.4	3.8	-4.9	0.2	57.4	1.7	-5.3	0.4
Top rock	35.4	3.8	-2.4	0.9	37.8	3.3	-1.4	1.0
Bottom rock	32.6	5.8	-1.9	0.9	34.8	5.8	-0.4	1.3
Deep crevice	17.5	7.1	0.9	0.9	15.2	1.4	4.6	1.5

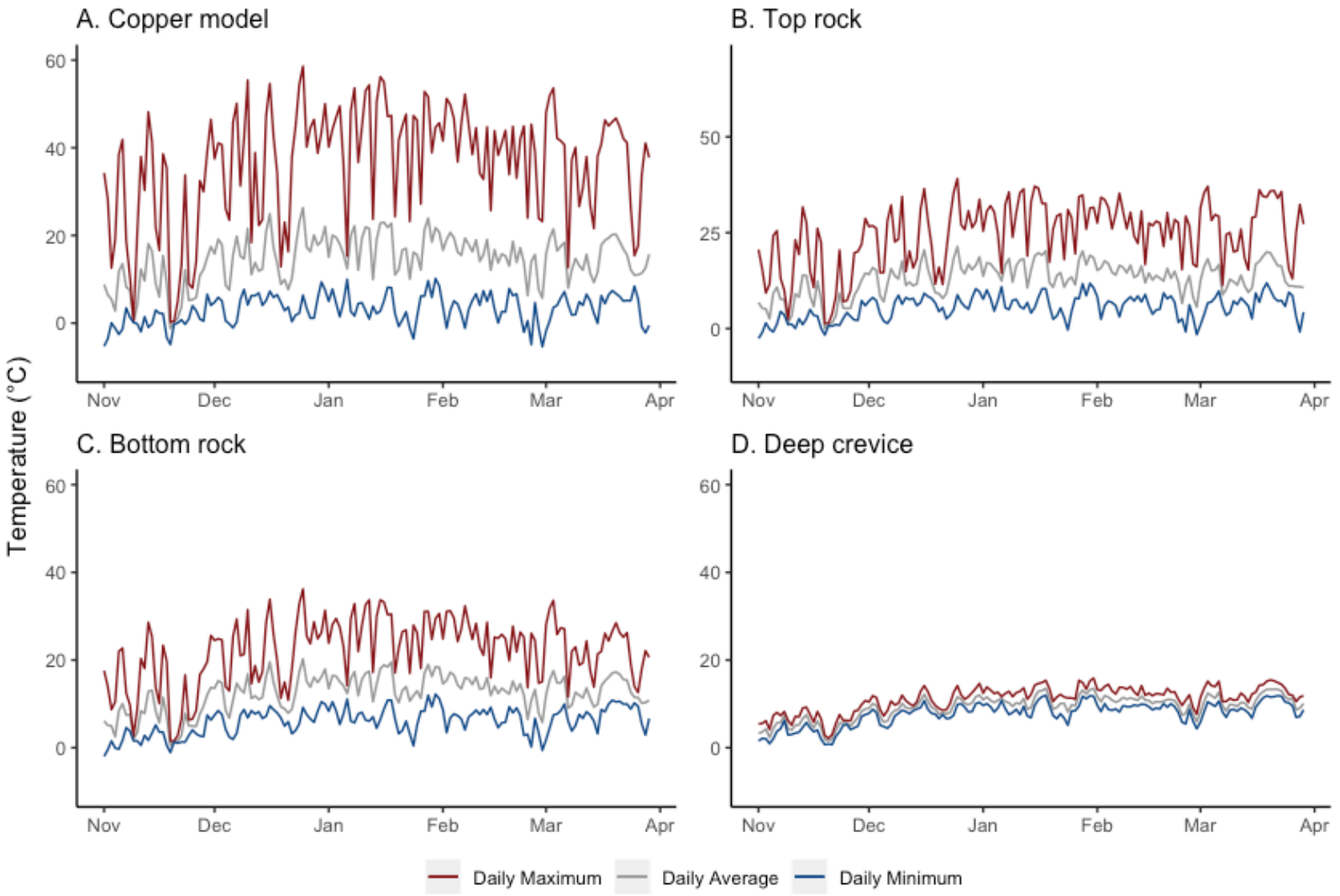

Figure 2.4 Microhabitat temperatures available to orange-spotted geckos during the spring and summer of 2018/19. iButton temperature loggers were placed in four different microhabitat positions (Copper model, Top rock, Bottom rock and Deep crevice) in five different locations. These four figures display the mean daily maximum, daily average and mean daily minimum temperatures for each of the microhabitat positions. I averaged the daily measurements for each of the four microhabitat positions across the five locations to get one value per microhabitat position per day.

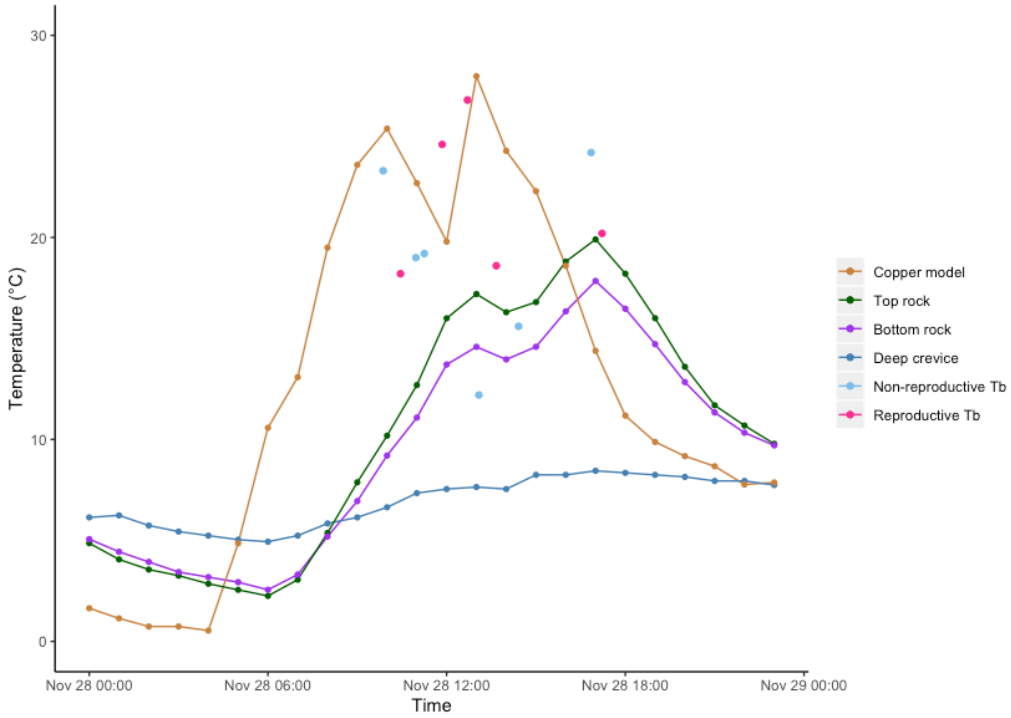

Figure 2.5 The relationship of all four microhabitat positions at one location on a sunny day over a 24-hour period. Geckos caught on the same day are presented with their recorded body temperature upon capture. Geckos were caught underneath surface rocks in similar positions to the bottom and top rock data loggers.

2.3.2 Relationship between gecko skin temperature and rock temperature

All rock temperatures in this section represent the top of the retreate that the gecko had occupied, similar to the top rock location. These temperatures were recorded with a mini-IRT device and will be refered to as “rock temperatures” from here on. Of all gecko captures, 95% occurred when air temperatures ranged from 9.5 to 19.2°C. Gecko skin temperatures by day varied from 8.0 to 29.6°C whereas rock temperatures varied more widely (5-39.6 °C; Fig 2.6). When rock temperatures were below 20°C gecko skin temperature was often warmer, while the opposite was apparent when rock temperatures surpassed 25°C (Fig 2.6). Consequently, the GAM shows that rock temperatures do influence gecko skin temperature ($F_{3.327, 4.147} = 44.83$, $p<0.001$) in that skin temperature increases consistently with rock temperature in an almost linear relationship until around 25 °C, where the relationship flattens out as rock temperature continues to increase and skin temperature does not. The proportion of variance that was explained by this model is 77%, so the model does an excellent job of

representing the relationship between gecko skin temperature and the variables in the model. Reproductive status impacts the spot body temperature of geckos (t_{19} = 36.78, p < 0.012) in that reproductive females have higher skin temperatures than other adults. This is supported by absolute measurements of gecko skin temperatures (Table 2.2). Lastly, season and time of day do not impact the skin temperature of geckos (F_{1}=0.186, p=0.667; $F_{1.0,1.001}$=1.96, p=0.166 respectively).

Rock temperatures influenced the skin temperatures of males and non-reproductive females ($F_{9.1639, 0.3641}$ = 52.64, P<0.001). Gecko skin slowly increases with rock temperature with an almost linear relationship (Fig 2.7). Skin temperature of reproductive females is also significantly affected by rock temperatures ($F_{3.089,3.873}$ = 23.16, P< 0.001). In this relationship, gecko skin temperature is higher than rock temperatures when the rocks are between 10-15°C and cooler than the rock temperatures when the rocks surpass 30°C (Fig 2.7). The model of reproductive females explains 73.4% of the proportion of variance while the model of the data and the model of non-reproductive geckos explains 80% of the proportion of variance. Lastly, reproductive female geckos have higher maximum, minimum and average skin temperatures when compared to non-reproductive females and males (Table 2.2).

Table 2.2 Absolute, maximum, average, and minimum skin temperatures of orange-spotted geckos caught during surveys

Reproductive Status	**Maximum skin temperature**	**Average skin temperature**	**Minimum skin temperature**
Other adults (n=36)	27.5	19.1 ±0.9	8.0
Reproductive females (n=37)	29.6	21.6±0.8	11.2

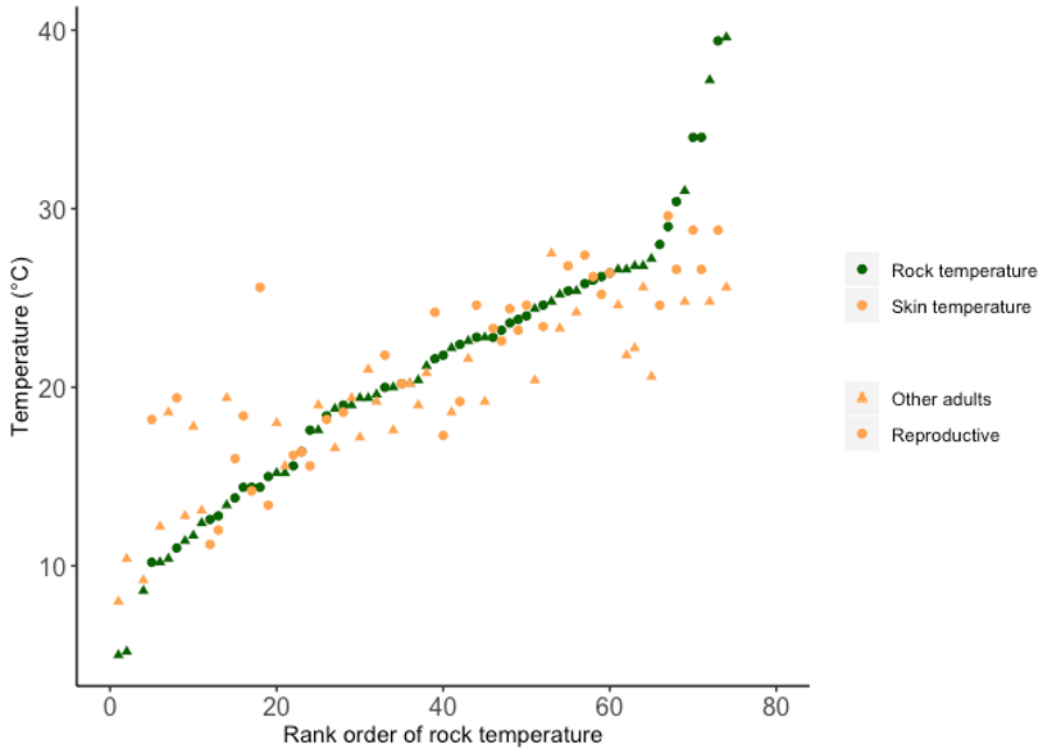

Figure 2.7 Skin temperature of individual orange-spotted geckos compared with the temperature of the underside of of their occupied rock. Measurements include historical data taken in February 2017 as well as data recorded during my spring/summer field season.

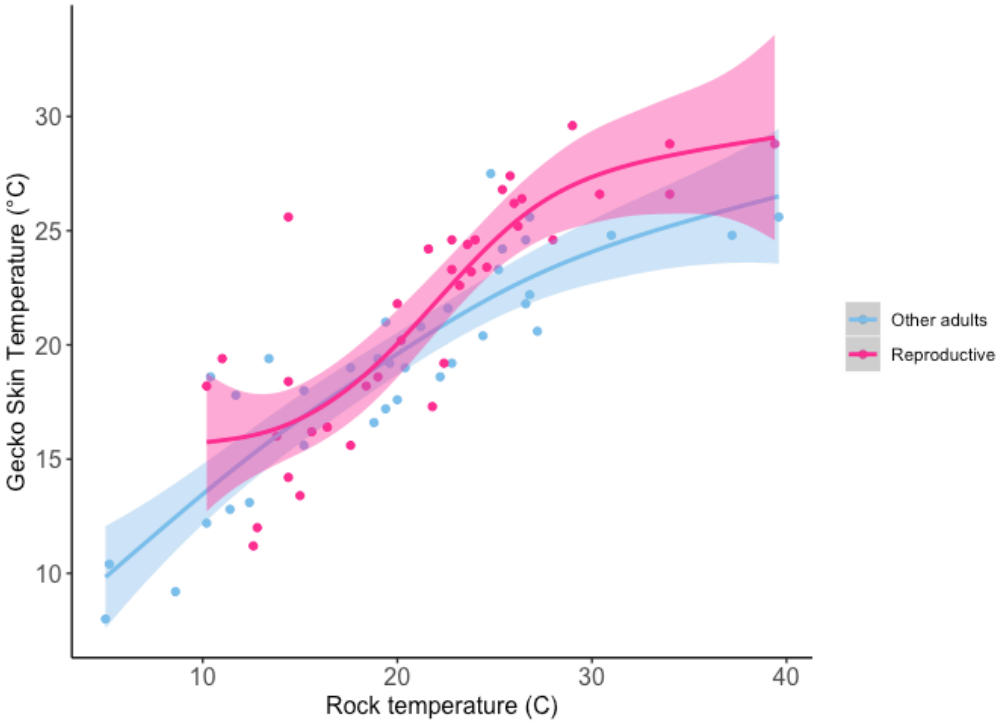

Figure 2.6 The fitted values from two generalized additive models, with their associated confidence interval shading. These compare the relationship between gecko skin temperature and the temperature of the underside their occupied rock, between reproductive females and non-reproductive females and males (other adults).

2.3.3 24-hour snapshot of an individual orange-spotted gecko monitored via a miniaturised bio-logger

I was able to retrieve one gecko with a bio-logger still attached. The individual was a pregnant female with a snout to vent length of 89 mm, a vent to tail length of 44 mm, that weighed 15 g. The gecko's movement did not appear to be impaired by the bio-logger or VHF transmitter as the lizard's gait did not change after the devices were added. When I removed the tape that attached the devices to the gecko it came off easily, and I could not see any adverse effects on the gecko's skin. The results from the single successful bio-logger trial show that this individual reached a maximum temperature of 26.5°C in the early afternoon and a low of 4.0°C overnight (Fig 2.8). From 2:19-2:35 pm the gecko's body temperature drops from 25°C to 16°C. Top rock and copper model data loggers from different days but at similar temperatures and times only change by 1-2°C over an hour. The temperature in the latter part of the night (between midnight and 6 am) was quite stable.

Figure 2.8 Temperature recorded by a miniaturised bio-logger monitoring the body temperature of a free roaming orange-spotted gecko over a 24-hour period. The hours of darkness were from 9:00 pm to around 7:00 am.

2.4 Discussion

The five microhabitats provide a wide range of temperatures for geckos throughout the summer. These locations provide refuge from extreme temperatures, in that at least one location (rock crevices 20-40 cm deep near gecko sightings) did not reach temperatures that surpassed 25°C at any point in time. Additionally, only one deep crevice location recorded a temperature that was below 0°C and the average absolute minimum temperature for all four crevice locations was above zero (0.9°C; Table 2.1). These microhabitats also heated and cooled at different speeds allowing geckos access to warmer temperatures earlier in the day and later into the night depending on the microhabitat that they utilised. Gecko skin temperatures did not reach temperatures as high as the nearby rocks as no skin temperatures surpassed 30°C. Pregnant female geckos maintained higher skin temperatures than other adults, and season had no effect on skin temperatures for pregnant females or other adults.

2.4.1 Available temperatures in orange-spotted gecko habitat

The temperatures recorded in orange-spotted gecko habitat are more variable than those recorded in the habitat for lower-elevation sites for *Woodworthia* geckos in Otago even though temperatures were recorded during the same seasons. Rock et al. (2000) recorded minimum and maximum microhabitat temperatures at two habitats of *Woodworthia* geckos, one in Alexandra (a lower-elevation near-continental climate) and the other at Macraes (a mid-elevation sub-alpine environment) during the austral spring and summer of 1996. At these two sites temperatures never went below -1°C and the warmest top rock recording was 37°C. Temperatures that I have recorded (during the austral spring and summer of 2019) in orange-spotted gecko habitat are almost 5°C cooler than temperatures recorded at these lower elevation habitats while the maximum temperatures recorded at top rock positions are similar. Even during the warmest part of the year, orange-spotted geckos experience colder temperatures than lower-elevation populations of other New Zealand geckos.

From international examples, Bouazza et al. (2016) used 16 data loggers left in the field from March to August 2012 and 2013 (which is equivalent to early boreal spring to late boreal summer) to record temperatures in the habitat of the Atlas day gecko. These loggers were

glued to the surface of rocks in various microhabitats, the exact positions of which are not described in the study. These loggers were programmed to record a temperature every 20 min. The study presented the results as mean monthly values, which limits my comparison as I do not know the absolute low and high temperatures recorded at the site. None the less, the lowest monthly mean was 3°C while the highest monthly mean was 39°C degrees. In another example, Darwin's ground gecko, the southernmost gecko found in Argentina, habitat has been shown to range from -5.9-59.5°C when recorded during the austral summer (Weeks and Espinoza 2013). In that study iButtons were placed in known gecko retreats, such as under surface rocks, from 9 January 2010 to 6 January 2011 and iButtons were programmed to record a temperature every hour. These methods are very similar to how I recorded temperatures at the orange-spotted gecko habitat, and the Darwin's ground gecko habitat is cooler by only 0.4°C. However, data were collected from orange-spotted gecko during the spring and summer and it is likely that these microhabitat positions will reach an even lower temperature over winter. This shows that on a global scale, orange-spotted gecko habitat reaches extreme temperatures when compared to habitats of other cold-adapted geckos.

Fortunately, the combined microhabitats that are available to orange-spotted geckos provide shelter from these extreme temperature swings. Copper model positions are the most exposed and, as a result, heat up rapidly when compared to all other microhabitat locations (Fig 2.5). This microhabitat could provide an excellent basking location where geckos can quickly increase their body temperature early in the day while the rest of their environment warms. Gibson et al. (2015) came to a similar conclusion studying the effect of retreat type on basking in korero geckos in which they state that high heating rates of copper models suggest that geckos may use them as initial basking locations while the rest of their environment is still cold. Then as temperatures rise and more sheltered retreats reach warm temperatures geckos will no longer need to bask and can utilise better-protected retreats such as those represented by the top rock and bottom rock positions (Fig 2.4; Fig. 2.5). Similar behaviour has been observed in alpine invertebrates that bask in the sun in the mornings but then use heated retreats, such as vegetation or surface rocks, later in the day (Sømme 1989). In the habitat of the Atlas day gecko, large surface rocks maintained their heat for long periods of time allowing geckos to

engage in prolonged periods of thermoregulation by keeping close ventral contact to these surface rocks (Bouazza et al. 2016). As a result, gecko body skin temperatures had a high correlation with surface rock temperatures, even when the air temperature was low. Orange-spotted geckos could be implementing the same strategies, using the top and bottom rock locations which are more stable than copper models in order to maintain their heat longer into the evening (Fig 2.5).

Warm retreats are important locations for ectotherms as they provide hot but not extreme temperatures, shelter from the elements and protection from predators (Kearney and Predavec 2000; Webb and Shine 2000). As a result, these warm retreats have large benefits for ectotherms. For example, rocks of moderate thickness allow garter snakes to not overheat while allowing them to spend more time at their preferred body temperature (Huey et al. 1989). For invertebrates, warmer refuges allow for faster development in spiders in eastern Australia (Goldsbrough et al. 2004). In lizards warmer refuges at night allow for higher levels of mobility, giving them a better chance of catching prey (Aguilar and Cruz 2010). As a result, these top and bottom rock positions likely play an important role in orange-spotted gecko thermoregulatory behaviour by providing a safe environment in which the geckos can reach higher body temperatures.

Lastly, the deep crevices provide a very stable but relatively cool environment. This microhabitat may provide an excellent refuge for geckos during extreme weather, such as an overwintering location, or during extremely hot periods in summer months. Deep crevices are often used by ectotherms to avoid extreme temperatures. For example, the green anole (*Anolis carolinensis*) aggregates in deep crevice locations that maintain stable temperatures when surface temperatures fall below freezing (Bishop and Echternacht 2004). Additionally, female velvet geckos (*Oedura lesueurii*) lay eggs in deep crevice locations, which provide a more stable environment more suitable for embryonic development (Pike et al. 2010). As a result, retreats that are similar to deep crevice locations may be used by orange-spotted geckos to survive extreme temperatures in their alpine habitat.

2.4.2 Relationship between gecko skin temperatures and environmental temperatures

When looking at the general relationship between skin temperature and the temperature of the gecko's occupied rock, many geckos maintained higher body temperatures at lower rock temperatures, and lower body temperatures at higher rock temperatures (Fig 2.6; Fig 2.7). These trends are not surprising because ectotherms have preferred body temperature ranges that they will voluntarily tolerate. Once temperatures go beyond those ranges, also known as the voluntary thermal minimum or maximum temperatures, an individual will usually relocate to a location with a more suitable temperature. When an ectotherm's body temperature surpasses their maximum or minimum threshold (termed 'critical thermal maximum' and 'critical thermal minimum'), the individual will start to lose primary functions and eventually shut down. (Kearney and Predavec 2000; Angilletta 2009). Although the preferred range of orange-spotted geckos is not known trends from my data suggest it lies within the range between 8 and 29°C (Fig 2.6; Fig 2.7).

Reproductive female geckos often maintained skin temperatures that were higher than other adults. Reproductive females had higher maximum, average, and minimum recorded body temperatures and they often reached body temperatures above 25°C whereas other adults did not (Fig 2.7). It is also not surprising that reproductive geckos maintain higher body temperatures than males and non-reproductive females as it is common to see a higher investment in thermoregulation by reproductive ectotherms (Lourdais et al. 2013). Similar trends are well documented in the korero gecko at Macraes. Multiple studies have shown reproductive females to place a higher level of investment in thermoregulation compared to other adults which results in higher recorded body temperatures (Rock et al. 2000; Rock and Cree 2003).

Reproductive geckos may be choosing higher temperatures to promote the successful development of embryos. A study of korero geckos compared groups under cold and warm habitats in a laboratory study (Rock and Cree 2003). The study found that no geckos were able to produce viable offspring under the cold regime in which geckos were given access to basking temperatures that ranged from 12-19°C. This suggests that there is a minimal thermal requirement in order for successful gestation to occur (Rock and Cree 2003). Additionally,

increased body temperatures have been shown to result in a shorter gestation period for korero geckos (Rock et al. 2000; Rock et al. 2002; Penniket and Cree 2015; Cree and Hare 2016b). A reduced gestation period may be advantageous for the mother as it allows her to start another reproductive cycle more quickly allowing her to increase her reproductive output in the long term (Rock et al. 2002). It also reduces the physical burden as the mother spends less time supporting young *in utero* (Cree and Hare 2016b). Additionally, an early birth could help the offspring by giving them more time to develop fat stores before winter or by giving them better access to nutrients and preferred temperatures in summer (Atkins et al. 2007; Wapstra et al. 2010). All of these examples could be drivers behind the difference in body temperature between reproductive and other adult orange-spotted geckos.

The body temperature of both reproductive females, males and non-reproductive female geckos is surprisingly similar to other cold-adapted New Zealand geckos. In studies from 2000, and 2008 reproductive female korero geckos have had recorded average field body temperatures of 24.9 ±0.7 °C and 22.2± 0.9 °C, respectively, in January and February-March (Rock and Cree 2000; Rock and Cree 2008). Considering the standard error, current orange-spotted gecko body temperatures are very similar to korero body temperatures from 2008 and ca. 2°C cooler than body temperatures taken in 2000 (Table 2.2). Measurements are more similar for males and non-reproductive females where the 2008 study measured field body temperatures of 18.4 ±1°C for males and 21.0±0.8°C for non-reproductive females, which is similar to the average skin temperatures of 19.16±0.9 recorded in other adult orange-spotted geckos (Table 2.2; Rock and Cree 2000; Rock and Cree 2008).

I was expecting orange-spotted body temperature to be lower than the body temperatures of korero geckos at Macraes. I thought that cooler weather that is associated with the alpine habitat that orange-spotted geckos live in would limit their ability to reach body temperatures that are similar to lowland geckos. However, their body temperatures seem to be fairly similar at least on sunny days. One explanation could be a limitation of spot body temperature measurements. Spot body temperatures can only be taken from individuals that are found in the field and geckos are the easiest to find on warm days with little to no wind. As a result, these spot body temperatures only represent skin temperatures of warm geckos under

ideal conditions as geckos would be too hard to find in adverse weather. So, these results could just be showing us that ideal conditions in the high-altitude orange-spotted gecko habitat are similar to ideal conditions in the Macraes habitat, which results in similar gecko skin temperatures. In cold, wet or windy conditions, there may be a larger difference between the two groups of geckos and give us a better understanding of how these lizards are interacting with their environment. Using the methods that I developed future studies could use bio-loggers to obtain gecko skin temperatures under a range of environmental conditions and greatly increase our understanding of the relationship between skin temperature and environmental temperatures.

2.4.3 Successful retrieval of real-time gecko field body temperature using a miniature bio-logger

In this study, I developed a method that allowed for the successful retrieval of continuous body temperature data from a free-roaming orange-spotted gecko. I was only able to retrieve a single bio-logger due to timing and material constraints, but this method may prove useful for future research involving geckos and bio-loggers. The benefit of the bio-logger is that it allows the researcher to gain access to continuous rather than spot temperature recordings. Thus, the researcher has access to a multitude of observations that would be impossible to retrieve without the device. It also allows the collection of skin temperature data during extreme weather, giving us insight into the real lows and highs that are experienced by an individual. Relocating geckos in a scree and boulder field is difficult. Even with a VHF device, you cannot guarantee that the individual will be at the surface so that you can recapture it. Hopefully, future studies will be able to extend my methods to successfully record the body temperatures of free-roaming geckos. When compared against temperatures in available microhabitats we will have a much better understanding of the true relationship between orange-spotted gecko skin temperature and environmental temperatures.

Unfortunately, I was unable to return to the field to retrieve the microhabitat dataloggers that were recording when the bio-logger trace was active. As a result, I do not have access to microhabitat temperatures with which I can compare to the trace. However, the

gecko's body temperature changed 9°C in just 16 minutes while temperature recordings from dataloggers at similar temperature ranges and time of day shift by just 1°C an hour. So, there is some circumstantial evidence suggesting that the gecko was actively creating the temperature fluctuations seen in the trace (Fig 2.8). If my assumptions are correct and the quick changes in body temperature are due to active thermoregulation then this trace suggests that this gecko was reasonably active during the day. There are five significant spikes in body temperature, all of which take place during the day. The morning of 30 March, for example, has three significant spikes between the early morning to early afternoon. These changes could represent active thermoregulation, such as movements between basking locations and surface retreats as the gecko takes advantage of early morning warmth at surface temperatures, like those measured at copper model locations (Fig 2.5). This is especially interesting as the orange-spotted gecko is considered to be mostly nocturnal (Knox et al. 201 9). However, temperatures recorded by this miniature bio-logger suggest that there is still a considerable amount of activity taking place during the day. These temperature fluctuations are supported by my observations of orange-spotted geckos openly basking during the day. By monitoring these lizards with time-lapse trail cameras, I captured multiple individuals basking throughout the day (Chapter 3).

In conclusion, orange-spotted geckos experience a wide array of temperatures in their high-altitude environment. These geckos can use different microhabitats within this environment to avoid cold and hot extremes and stay within what I assume to be a preferred range of temperatures. Reproductive females maintained higher body temperatures than males and non-reproductive females. However, all geckos showed evidence of active thermoregulation when rock temperatures were high, suggesting that these geckos are quite active during the day, especially for a species that is considered to be nocturnal. These findings give us insight into the daily activities of orange-spotted geckos within their habitat. With this information, we can inform management practices so that they take place during temperature and weather windows in which orange-spotted geckos are likely to be active. For example, we know that pregnant females are thermoregulating when the temperature of rocks ranges from 15-30°C and air temperature ranges from 9.5 to 19.2°C. This activity is shown by temperature differences between skin and rock temperatures, and suggests that these pregnant females are

likely active at these temperatures. If we wanted to increase our monitoring success of this group of geckos, we need to time surveys so that they take place when rock and air temperatures are within these ranges. This study also highlights the importance of microhabitats and the varying temperatures that they provide for geckos. If microhabitats are disturbed or destroyed, geckos will lose their refuge from the extreme cold as well as some of their ability to thermoregulate at the surface. As a result, future management programs should focus on maintaining orange-spotted gecko habitat so that we do not disturb these integral microhabitats.

Chapter 3 The influence of weather on surface activity of alpine lizards, with evidence of diurno-nocturnal activity in orange-spotted geckos

3.1 Introduction

The study of daily activity patterns is central to understanding how animals interact with their environment. The period which an animal is active dictates the temporal niche that a species fills and thus influences the environmental and ecological conditions to which active individuals will be exposed (Mech et al. 1966; Terezow et al. 2008). Activity periods also influence the interaction of species by allowing them to use the same space at either the same or different times (Kronfeld-Schor and Dayan 2003). As a result, activity periods dictate the sorts of threats that a species experiences, whether these threats be from predators (Holomuzki 1986) or anthropogenic (Thiers et al. 2014). Finally, understanding activity patterns and how they relate to environmental conditions can help us predict how climate change might affect a species' activity (Tirado et al. 2018). How a species reacts to local weather conditions is exceptionally important to understand when studying ectotherms, because the ability of ectotherms to be active is dependent on temperature and other weather conditions in their environment (Angilletta 2009). However, monitoring ectotherms such as lizards within their microhabitats is complicated as many species are small, cryptic, and easily disturbed.

With recent advances in technology, trail cameras or camera traps have become an important tool in ecological studies as a way of remotely monitoring animals over prolonged periods. To date, studies employing trail cameras have predominantly involved larger mammals, and have included studies of movements (Kays et al. 2009), behavioural interactions (Lazenby et al. 2015; Allen et al. 2016), and the success of management interventions (Foster and Humphrey 1995; Donaldson 2007). For example, numerous studies In New Zealand have employed camera traps to monitor the presence of introduced mammalian predators including cats, stoats and hedgehogs (Glen et al. 2014; Glen et al. 2016). More recently, trail cameras have become prevalent in the study of small ectotherms, albeit recognising that these devices are not optimised to monitor these animals. Many camera traps use a passive infrared sensor

(PIR) that detects animals using a combination of heat and motion (Hobbs and Brehme 2017). These sensors are designed for animals that take up a significant portion of the frame and have a body temperature that is at least 2.7°C different from the surrounding environment (Rovero et al. 2010, Rovero et al. 2013). Unfortunately, small ectotherms, like lizards, take up a small amount of the frame and their body temperatures are not always sufficiently differentiated from the environment for a camera to sense the individual (Ariefiandy et al. 2013). Thus, small ectotherms trigger the device less consistently, making them more challenging to monitor.

As a direct result of their difficulty to monitor we still have a lot to learn about lizard activity patterns in New Zealand. Internationally, species have been considered to be diurnal (Vicenzi et al. 2019), nocturnal (Eifler et al. 2017), crepuscular (Moore et al. 2018), or bimodal (Treilibs et al. 2016). In New Zealand, activity periods are less clear. The *Naultinus* geckos are secondarily diurnal (Hare et al. 2007) and will not be discussed any further as my focus is on nocturnal New Zealand geckos. Many of these geckos have been considered as 'nocturnal' but recent work has demonstrated the potential for daytime activity (Flannagan 2000; Todd 2005; Frank and Wilson 2011; Gibson et al. 2015). Nocturnal activity comes with significant drawbacks, especially in cold climates, as temperatures at night are often suboptimal for locomotion (Cree and Hare 2016a). Consequently, it is not entirely surprising that some of these nocturnally foraging species have also been shown to bask in direct sunlight to attain higher body temperatures (Cree and Hare 2016b). For example, Gibson et al. (2015) used time-lapse trail cameras to confirm that Otago/Southland or korero geckos (*Woodworthia* 'Otago/Southland') at Macraes a sub-alpine grass covered, rocky habitat in eastern Otago bask during the day despite their nocturnal classification. Though there had been anecdotal reports of diurnal activity in this and some other New Zealand geckos, the study by Gibson et al. (2015) was the first to provide quantitative evidence of diurnal emergence in this genus. The authors also found that females basked longer than males and that these bring advantages in terms of shorter and more successful pregnancies (Rock and Cree 2003; Cree and Hare 2016b).

In the study by Gibson et al. (2015), time-lapse cameras equipped with night-vision were programmed to take photos at scheduled intervals throughout both day and night. As a result, these cameras have a better chance of monitoring small lizards as they do not rely on size of

the individual to trigger the collection of an image. However, this approach is very time intensive. Time-lapse technology generates hundreds of thousands of photos and, often, very few of those photos contain the target species (Hobbs and Brehme 2017). Additionally, using programmed intervals means that the subject might not always be caught at the start of its activity, so information on timing and the full routine of the activity period is limited. Lastly, time-lapse photos are often reviewed manually, which creates the possibility of input errors as reviewers process hundreds of thousands of photos (Swanson et al. 2015). One potential to lessen the burden that time-lapse cameras create is machine learning. This analysis uses computer programming to scan images for species of interest so that it does not need to be done manually. This technology is still relatively new and not entirely "user friendly"; studies to date are on large mammals that take up a greater proportion of the image, making it easier for the programming to recognise (Gomez et al. 2016; Norouzzadeh et al. 2018; Tabak et al. 2019). However, as technology improves, machine learning may be a useful tool for lizard monitoring.

Species of lizards that could benefit from better understanding of activity patterns via the use of trail cameras include those of the alpine zone. Of particular interest is the orange-spotted gecko (*Mokopirirakau* "Roys Peak"). This small, cryptic gecko lives in alpine regions of western and central Otago between 1150–1620 m a.s.l. Little is known about its emergence patterns, apart from the fact that it is active at night and is considered to be nocturnally foraging (Knox et al. 2019). Several species of poorly known skinks (*Oligosoma* spp.), all endemic to New Zealand, are also present in this habitat. The exact activity periods of these skinks are not known. Several other species of *Oligosoma* are diurnal, but in warmer parts of New Zealand *Oligosoma* species can be crepuscular or nocturnal (Freeman 1997; Hare et al. 2009; Dahirel et al. 2015; Cree and Hare 2016a; Hare et al. 2016). Continuous monitoring of the alpine habitat would increase our understanding of emergence activity for both geckos and skinks. For example, it would allow us to test whether both diurnal and nocturnal activity are present in each group of lizards and, if so, under what environmental conditions. Trail cameras are ideal for monitoring lizard activity in this remote alpine habitat for two reasons. First, as the site has limited to no vehicle access and is difficult to access on foot, researchers are unable to

be physically present on a frequent basis. Second, the same factors mean that there are low chances of the cameras being vandalised or stolen.

We can further increase our understanding of how these lizards interact with their environment by evaluating how weather influences their emergence activities. Lizards are usually more active when conditions are warm and sunny because warmer temperatures allow maintenance of high body temperatures, which promote physiological functions such as locomotion, metabolism, and reproduction (Angilletta 2009; Huey et al. 2009; Caldwell et al. 2015). Conversely, activity typically decreases when temperatures are cooler or strong winds or rain are present (Lettink et al. 2011). In a study involving field observations at Macraes, the number of observed grand skinks (*O. grande*) and Otago skinks (*O. otagense*) decreased as wind speeds increased, and researchers also saw fewer skinks when the habitat was wet, or snow covered (Coddington and Cree 1997). Similarly, Ortega et al. (2017) found that high wind speeds correlated with a significant decrease in the effectiveness of thermoregulation in *Iberolacerta aurelioi*, a high-altitude lizard from La Massana, Andorra, in the Pyrenees. Ortega et al. (2017) further surmised that wind reduces an individual's body temperatures, can increase desiccation, complicate the hunting of prey, and reduce daily activity.

In this chapter, I aimed to identify the primary activity periods (day vs night) and the environmental conditions that permit lizards (geckos and skinks) to be outside their retreat in an alpine environment. The only gecko at my study site is the orange-spotted gecko. In terms of skink taxa, the majority (~95%) of individuals are likely to be McCann's skink (*O. maccanni*), but Canterbury grass skink (*Oligosoma aff. polychroma* Clade 4) and Lakes skink (*Oligosoma aff.chloronoton* 'West Otago') are also present (Carey Knox, Wildlands, pers. comm.). Adult Canterbury grass skinks and juvenile Lakes skinks are very similar in size and shape to McCann's skinks. Because the resolution of my photos was not high enough to distinguish amongst species, I combined all skink observations.

I addressed several questions: (1) How does surface activity vary between day and night for geckos and skinks? I define surface activity as an activity where an individual is entirely or partially exposed so that it is visible on camera. I did not aim to describe activity that is underneath rocks or out of human sight. I predicted that geckos would be active on camera at

night and during the day, whereas I expected skinks to appear on cameras only during the day. (2) Within the activity period, how do microhabitat temperatures and other weather conditions influence the surface activity (including in potential basking positions)? I predicted that activity for both skinks and geckos would increase when temperatures are warm, and when strong winds and rain are not present. (3) When geckos and/or skinks are detected out of their retreats by trail cameras, what are they doing? How long can they be inferred to be active for, and how does their behaviour change with the period of emergence (e.g. between night-time and daytime)? Given that my trail cameras captured stills, not video footage, I was only able to infer what individuals are doing based on the difference in body positions between photos. (4) What species of introduced mammals are detected by trail cameras in the alpine lizard habitat, and is there any evidence of these species affecting lizards?

3.2 Methods

3.2.1 Monitoring emergence behaviour

During periods within the austral late spring to early autumn, I collected photos of lizards by monitoring locations where I previously found pregnant orange-spotted geckos, in scree slopes interspersed and surrounded by tussock. Monitoring periods consisted of four different sessions: 28 November 2018 to 25 December 2018, 20 January to 28 January 2019, 20 February to 7 March 2019, and 15 - 28 March 2019. I used two types of cameras throughout the field season, the KeepGuard KG -780EB (ScoutGuard, USA) and the Reconyx HC 500 Hyperfire (Reconyx Inc., Holmen). The first two photo-monitoring periods used the KeepGuard KG -780EB cameras. However, it became apparent that these cameras did not take high-quality photos at night (the photos were either too grainy or overexposed, such that I was unable to see whether lizards were present). I was able to use some of the nocturnal footage from the KeepGuard cameras, but the total number of observations at night was reduced by the photo quality. KeepGuard cameras took high-quality photos during the day, so I was still able to obtain information on day-time emergence of both skinks and geckos. In the last two periods, I only used the Reconyx cameras which took higher quality nighttime and photos.

I placed eight cameras facing different retreats in which I had found pregnant female orange-spotted geckos during my first field survey in October 2018 (Chapter 2). At each location, I mounted one camera on a 500 mm black steel waratah, which was placed no more than 1 m away from the focal rock. Some cameras were placed close to large rocks to maximise the chances of observing geckos basking beside the retreats. Other cameras had a broader view of the habitat with the aim of observing geckos moving across the rock surfaces. To attach the camera to the waratah, I used swivel inserts. These devices have a ball and socket joint that allows the user to adjust the camera's angle of view. The swivel insert can be left connected to the waratah in the field so that the same point of view can be maintained throughout the monitoring period, even if the camera has been temporarily removed. I programmed all eight cameras to take one photo every minute until they ran out of battery power.

For the two final monitoring sessions, I replaced the KeepGuard cameras with Reconyx cameras. Only five Reconyx cameras were available for the third trip, and six for the fourth trip. As a result, I chose five locations, from the previous eight, that provided a good balance of habitat and field of view to keep the types of habitat that were monitored consistent across all monitoring sessions. Fortunately, the Reconyx cameras have long battery life, and the five cameras were able to take more photos than the eight KeepGuard cameras. I placed the Reconyx cameras in locations where the KeepGuard cameras had recorded gecko activity to attempt to maximise the observations from the reduced number of cameras. I also programmed the Reconyx cameras to take a photo every minute until the batteries died or the memory card was full. Fortunately, the Reconyx cameras allow for the PIR sensors to be turned off, and the cameras functioned as programmed for their entire battery life.

To help analyse my photos, I used Timelapse (Greenberg and Godin 2015), an image-analysis programme that streamlines the data collection from large numbers of photos. Timelapse organises all of the photos into a slideshow-like viewing screen. Timelapse then allows the user to generate data by typing, selecting from a list of customised choices, or by clicking on objects in the image to count them. This software still requires the user to analyse all of the photos manually, but it makes this process easier and faster. Using this software, I recorded counts of geckos and skinks, observations of weather including fine (i.e. sunny or

partially cloudy days), rain (any presence of rain on the rocks), snow (presence of snow), wind level (none - the vegetation was not moving at all; light - vegetation was slightly moving in the breeze; or strong - vegetation was significantly moving in the wind), and observations of any mammalian predators. Movement in vegetation was observed by comparing a photo with the next photo taken by the camera. The wind would move vegetation so that the leaves of the plant would be in a new location in the second photo when compared with the previous one. The amount that vegetation swayed determined the category of wind strength for that photo. I used visible weather conditions instead of the NIWA Virtual Climate Network because NIWA data interpolates weather across large distances from weather stations and is likely to be less accurate for small, high-elevation locations, like the QLA habitat studied here (Case et al. 2016). I was also able to identify individual lizards when they were recorded in several photos in a row. I did this by assuming that I was observing the same individual due to its position and movement across a number of photos. This allowed me to monitor the duration that individuals were active on the surface. Once the individual left the frame for more than 10 min, I considered it to be a new period of emergence . Timelapse then exports all observations into a CSV file which can be easily accessed by statistical software.

3.2.2 Temperatures of available microhabitat across a calendar year

I used the same microhabitat temperature data that I gathered in Chapter 2. To obtain these data I placed four loggers in different microhabitats at five different locations. The microhabitats include the copper model position, top rock, bottom rock and deep crevice. Please see Chapter 2, Methods, “Temperatures of available microhabitat across a calendar year” for more specific information on where and how I placed the loggers in the gecko microhabitat.

3.2.3 Statistical analysis

First, I organised gecko and skink observations into counts that matched the time intervals for the temperatures recorded by the data loggers. The cameras took a photo every minute, whereas the dataloggers recorded temperatures every hour, I combined camera

observations into 1 h blocks. I summed the number of lizard observations in each hour, giving me a count of lizard sightings per hour (note, these are sightings rather than the total number of different individuals). I then categorised 'weather' as fine = 1, rain = 2 and snow = 3. For wind, no wind = 0, light wind = 1, and strong wind = 2 and I took the mean of each variable within the hour block. To assign temperature values to each photo observation I first calculated the mean temperature recordings across the five datalogger locations for each microhabitat. I then matched the hourly camera observations to the corresponding mean temperature from the dataloggers by matching up the date and time that the photo was taken. In the end, each camera observation had a matching mean temperature from each of the four microhabitats. I only used temperatures from two of the four microhabitats; these were the copper model and bottom rock temperatures. I excluded the deep crevice microhabitat as I felt it would not influence emergence activity. I excluded the top rock temperatures because they were too similar to bottom rock temperatures (with a correlation coefficient of 0.98). When both of the rock microhabitats were included in the analysis, they caused my models to have a high variance inflation factor. I assumed that lizards would be on flat against surface more than they would be pressing themselves up against a top rock, so I chose to include bottom rock temperatures over top rock temperatures.

I conducted all the analyses in R studio (R Core Team 2018). For the relationship between microhabitat temperature and counts of lizards (for each species, separated by day and night), I initially attempted to model the data with Poisson-distributed generalised linear mixed models (GLMM). However, these led to a high overdispersion parameter given the large number of photos where no lizard was present. I therefore changed to using zero-inflated, negative binomial, generalised linear mixed-effects models (ZINB) within the package glmmTMB; ZINB models are suited to data that are over-dispersed with a large number of zeros (Yau et al. 2003). Sightings of geckos or skinks was the response variable, with temperatures recorded by copper models, temperatures recorded by bottom rock loggers, wind levels, and weather types as predictor variables. The models also included camera location as a random effect to account for the multiple photos taken from the same position. This resulted in three

models, one containing diurnal sightings of skinks, one containing diurnal sighting of geckos, with the last containing nocturnal sightings of geckos.

I then constructed three more models, containing presence-only data for each species (i.e. camera observations where a gecko or a skink was present), separated by activity period. These models were constructed to understand which of the environmental variables influence geckos when they are present. A higher count of geckos implies that geckos prefer the environmental variables at the time more than when counts are low. These models differ from the previously described models, which attempted to identify the environmental conditions that allow for emergence in the first place. For these, I ran generalised additive mixed models (GAMM) within the package MGCV and negative binomial GLMMs within the package lme4. As before, these models had gecko or skink counts as the response variable; temperatures recorded by copper models, temperatures recorded by bottom rock loggers, wind levels, and weather types were predictor variables, and camera location was a random effect. I compared model performance between the GAMM and the GLMM models for each analysis based on their Akaike information criterion (AIC), R^2, and F statistic. The AIC metric provides a powerful tool for comparing non-nested models, allowing me to infer whether the GAMM or GLMM was better at representing the data (Posada and Buckley 2004; Aho et al. 2014).

I chose to examine both GAMM and GLMM models as the relationship with some (but not all) environmental variables appeared non-linear. The strength of the GAMM is its ability to describe non-linear relationships between the response and explanatory variable; however, this flexibility results in a less robust test statistic. The GLMMs provide more robust test statistics but do a worse job of describing relationships that are non-linear (Guisan et al. 2002; Bolker et al. 2009). In an attempt to make the best use of the strengths of each model type, I selected GAMMs as a better representation when the relationships were non-linear. When the outputs from the GAMM and GLMM were very similar I selected the GLMM, as it is a less complicated model and the smoothed term of the GAMM was not necessary to explain the relationship between variables.

3.3 Results

3.3.1 Lizard surface activity

In total, I collected 370,766 photos of orange-spotted gecko habitat. Of those photos, only 3,733 contained at least one gecko and 1,930 contained at least one skink. For the orange-spotted gecko, I observed 2,936 photos containing nocturnal gecko activity. The most prolonged period of activity was 7 h 54 min, while the mean activity length was 22 min with a standard deviation of 64.74 min. When geckos were present at night, they displayed two different types of activities. The first was mobile where individuals would appear to be moving across their habitat, returning to or leaving a crevice. The second was more sedentary. Individuals would sit at the entrance to a crevice, partially exposed with their head facing out of the crevice entrance. These individuals would remain in those spots for hours, and some were present at the surface for a large portion of the night. Some individuals would reposition themselves every 20 to 30 min, while others would remain in the same position for over an hour. When individuals moved, they would change the direction they were facing, move to a slightly different spot at the entrance of their retreat, and move their head from side to side, looking as though they were scanning their nearby environment. Based on the number of gecko sightings per hour there was no specific time of the night that contained noticeably more gecko sightings.

In one notable observation, an individual was present on the surface at midnight on the 28 March 2019 when mean copper model temperatures reached -0.8°C, although mean temperatures were warmer at top rock (2.3°C) and bottom rock (6.1°C) microhabitats. So, it is reasonable to assume that the body temperature of this individual was between -0.8 and 6.1°C. When the individual was at the surface it was partially exposed with its head and a portion of its torso visible on screen. The gecko remained close to its crevice and only moved to reposition its body and glance around its habitat. I could not discern any specific reason behind why this individual would be exposing itself at these low temperatures.

I observed less gecko activity during the day. Only 758 images contained diurnal gecko activity. The longest recorded period of activity was 84 min, while the mean activity length was

15 min, with a standard deviation of 21.45 min. When geckos were basking, I never saw an individual more than a body (snout-vent) length away from their retreat. Individuals basked in short spurts where they would move between an exposed basking position to the cover of a nearby crevice. When individuals exposed themselves to the sun, they would continuously reposition themselves. The repositioning included changing the direction they were facing, increasing or decreasing the amount of their body that was in the sun, changing what body parts were in the sun, and moving to different locations within the rock on which they were basking. Common basking positions included half and full abdomen basking, basking with only the head in the sun, and mostly full-body basking (Fig 3.1). Based on counts of diurnal gecko sightings there were noticeably more sightings from 7:00 to 11:00h.

For the skinks (*Oligosoma* spp.), I did not observe nocturnal activity. The most extended period of activity was 63 min, while the average activity period was just 3 min, with a standard deviation of 6.40 min. When skinks were present on the surface, they were very mobile. Skinks were often only in the frame for one to two photos in a row and even on these short recordings, individuals changed positions between frames. When skinks did remain in the frame for more extended periods, they were always moving and repositioning themselves. Individuals would move to slightly different locations on the rock, change which position they were facing, or move across the habitat in order to reach direct sunlight. Skinks were almost always in direct sunlight and were rarely observed under the cover of surface rocks. Skinks were observed throughout their habitat and were not always adjacent to a large retreat or crevice. Based on the number of skink sightings per hour there was noticeably more sightings at 10:00 and 11:00 and from 15:00-17:00 h. I saw no interactions between lizards of any kind.

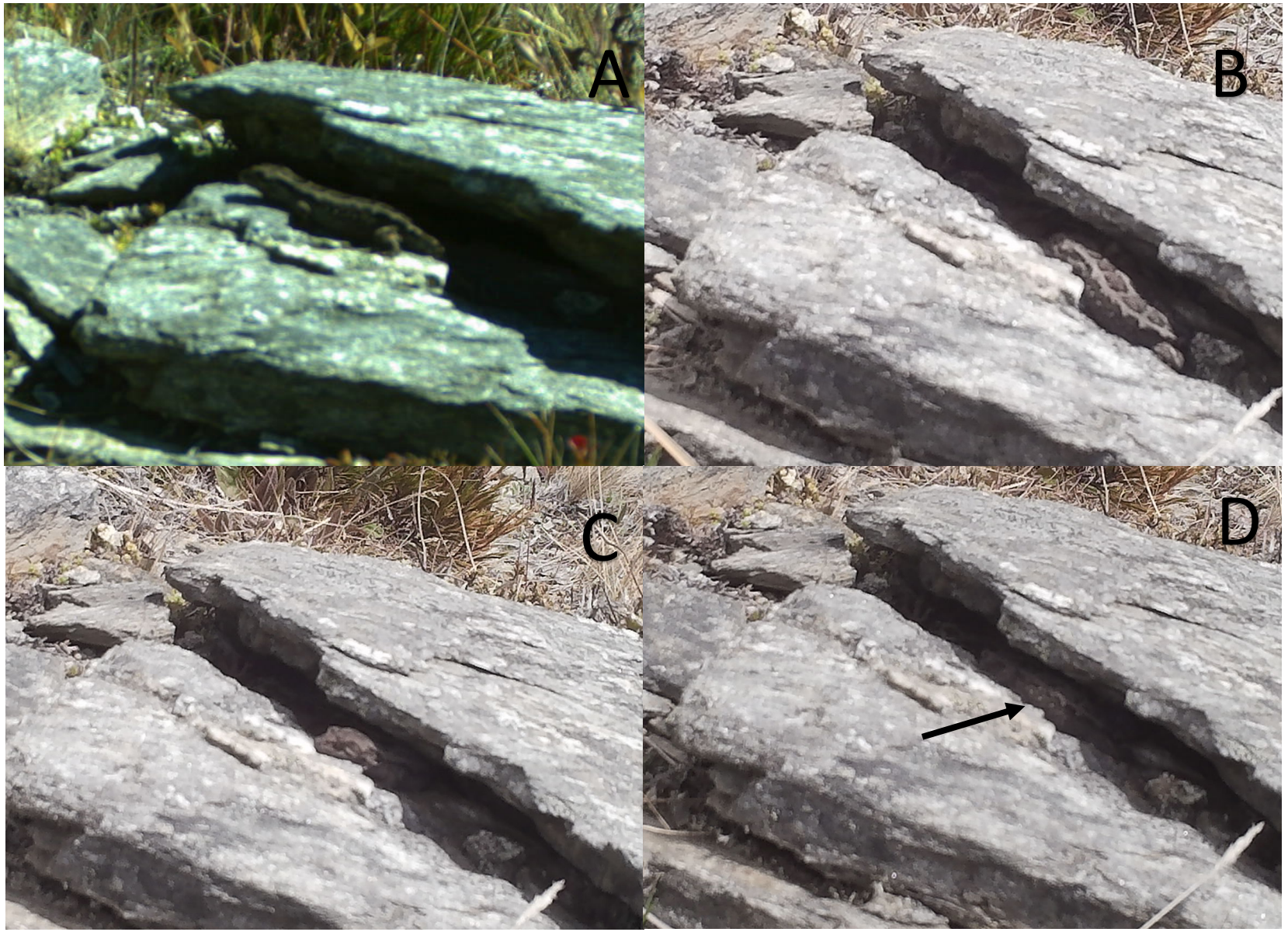

Figure 3.1 Examples of basking behaviour in the orange-spotted gecko at the QL-A site. A is a gecko with 80% of its body exposed to the sun. B is a gecko with its entire abdomen exposed. C is a gecko with only its head exposed. D is a gecko under the surface rock near the crevice entrance. These photos were taken on different days, but it is possible that it is the same gecko.

3.3.2 Relationship between environmental conditions and lizard emergence

For geckos, results from the ZINB model show that temperature of the copper model microhabitat, wind levels and presence of snow and rain significantly affected gecko sightings during the day. Gecko sightings increased as copper model temperatures rose, but no geckos were observed when copper models surpassed 40°C. Additionally, no geckos were observed in snow or strong winds, and the presence of rain greatly decreased gecko sightings (Table 3.1). At night, bottom rock temperatures affected observations of gecko presence, as did strong winds (Table 3.1). Sightings increased as temperatures of the bottom rocks increased. No geckos were observed in the snow and sightings of geckos decreased when strong wind was present. For the skinks, the daytime model of skink sightings showed that copper model temperatures, bottom rock temperatures, and presence of rain and snow all had a significant effect on skink counts. Sightings of skinks increased as temperatures at the copper models and bottom rock locations rose while presence of rain and snow decreased the number of sightings. In general, the fit of the models was quite poor. The marginal R^2 for all three models were 0.3 or below, which suggests that there are other factors at play that are not represented by the model (Diurnal gecko: R^{2C}= 0.643, R^{2M}=0.267; Nocturnal gecko: R^{2C}= 0.597, R^{2M}=0.291; Diurnal skink: R^{2C}= 0.343 R^{2M}=0.300).

Table 3.1 Results from ZINB models using the entire dataset (photos when geckos were present and absent) for emergence of lizards in the QL-A habitat. Significant results are in bold.

	Diurnal emergence of geckos				**Nocturnal emergence of geckos**				**Diurnal skink emergence**			
	DF	X^2	p	R^2	DF	X^2	p	R^2	DF	X^2	p	R^2
Copper model temperature	1	15.609	**< 0.001**	0.52	1	0.0410	0.839	0.56	1	39.178	**< 0.001**	0.29
Bottom rock temperature	1	2.105	0.146		1	12.550	**< 0.001**		1	13.531	**< 0.001**	
Wind	1	6.889	**0.009**		1	5.194	**0.020**		1	0.356	0.637	
Weather	2	19.502	**< 0.001**		2	2.821	0.244		2	123.943	**< 0.001**	

3.3.3 Nocturnal activity of geckos

A table of outputs from both the GAMM and the GLMM can be found in Appendix 3. In this section and the two that follow, I report only the results of the selected models. Geckos were seen when mean temperatures of copper models ranged between -0.8 and 14.6°C (Fig 3.2). Mean temperature at the copper model microhabitat significantly influenced the observation of geckos at night in a non-linear fashion (GAMM: X^2=10.39, DF= 2.57 p=0.02), but not in a linear fashion (GLMM: X^2=2.89, DF=1, p=0.089). Despite the GAMM having more support than the GLMM (ΔAIC=0, adjusted R^2=0.56; ΔAIC= 16.08, R^{2m}= 0.07 R^{2c}=0.15 respectively) the curved relationship is weak (Fig. 3.2) and should be treated with caution

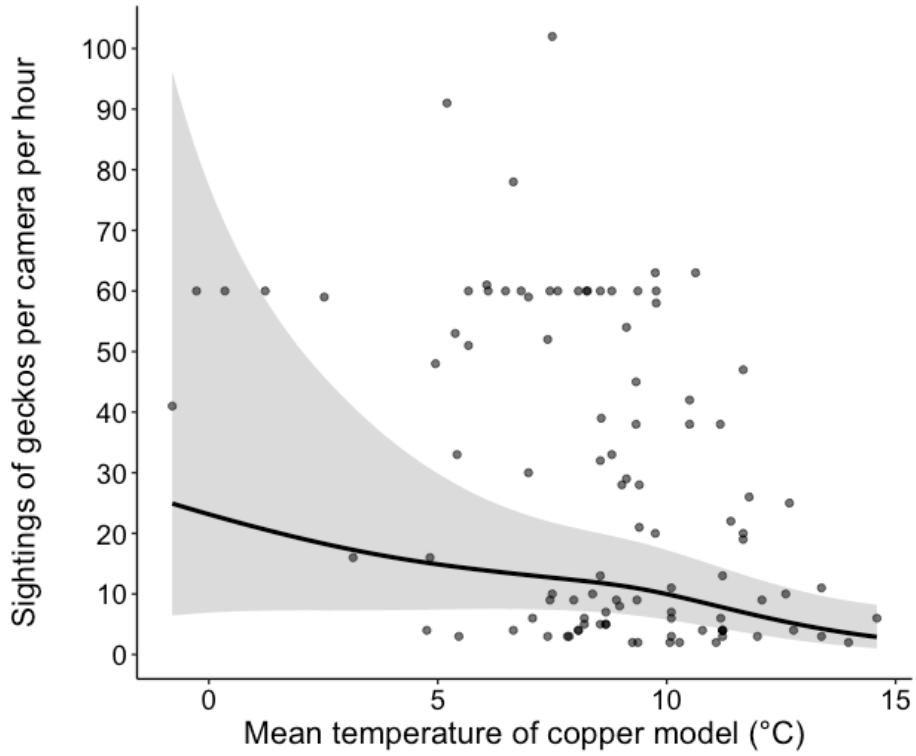

Figure 3.2 Relationship between gecko sightings and mean temperatures of copper models described by a GAMM. Copper model temperatures are averaged across all five microhabitat locations. Each point is the total number of photos that contains a gecko in an hour period. Zero values were not included, and the shaded area represents the confidence interval.

3.3.4 Diurnal activity of geckos

Geckos were seen by day at mean temperatures of copper models between 3.3°C and 39.3°C (Fig 3.3 A). The temperature of the copper model influenced diurnal counts of geckos in

both the GAMM and GLMM. Ultimately the relationship was not linear (Fig 3.3 A) and the GAMM had a stronger fit to the data when compared to the GLMM (ΔAIC= 0, adjusted R^2=0.77; ΔAIC= 11.95 , R^{2m}= 0.45 R^{2c}=0.58 respectively), so it was best described by the GAMM (DF= 4.397, X^2= 38.87, P=<0.001). Temperature of the copper models appears to have little impact on observations of gecko presence until around 20°C. Between about 20°C and 30°C, the number of gecko observations increases and above this temperature they decrease (Fig 3.3 A). A GLMM better explained the relationship between diurnal gecko counts and bottom rock microhabitats when compared to a GAMM as the relationship is linear (Fig3.3 C; DF=1, X^2=30.357, P<0.001). As temperatures at the bottom rock microhabitat increase counts of geckos slowly decrease (Fig 3.3 C). Additionally, the GLMM showed a relationship between wind strength and gecko presence. Gecko sightings decreased as wind strength rose (DF=1, X^2=5.503, P =0.019). Weather was not included in the analysis of daytime activity because geckos were only found on fine warm days.

3.3.5 Diurnal activity of skinks

Skinks were seen during the day at mean temperatures of copper models between 12.8°C and 51.0°C (Fig 3.3 B). As for observations of diurnal gecko activity, skinks were also only seen on warm sunny days. Temperatures at copper model and bottom rock locations significantly influenced observations of skinks during the day. The relationship between skink sightings and temperature at the copper model microhabitats was better described by the GAMM as the relationship is not linear; the GAMM had a lower AIC and a higher R^2 when compared to the GLMM (ΔAIC= 0, adjusted R^2=0. 51, ΔAIC= 12.89, R^{2m}= 0.32 R^{2c}=036. Respectively; Fig 3.3 B). The relationship shows that higher counts of skinks are seen between 12.8°C and 25°C, and greatly decrease as temperatures surpass 30°C (EDF=5.23, X^2= 78.91, P=<0.001; Fig 3.3 B). The relationship between bottom rock microhabitat temperatures and counts of skinks is positive; whereby counts of skinks slightly increase as the temperature at bottom rock locations rise (Fig 3.3 D).Even though the GAMM had a slightly better fit (as described above) the GLMM was chosen to describe these variables as the relationship is linear (df=1 X^2= 24.59, P=<0.001; Fig 3.3 D).

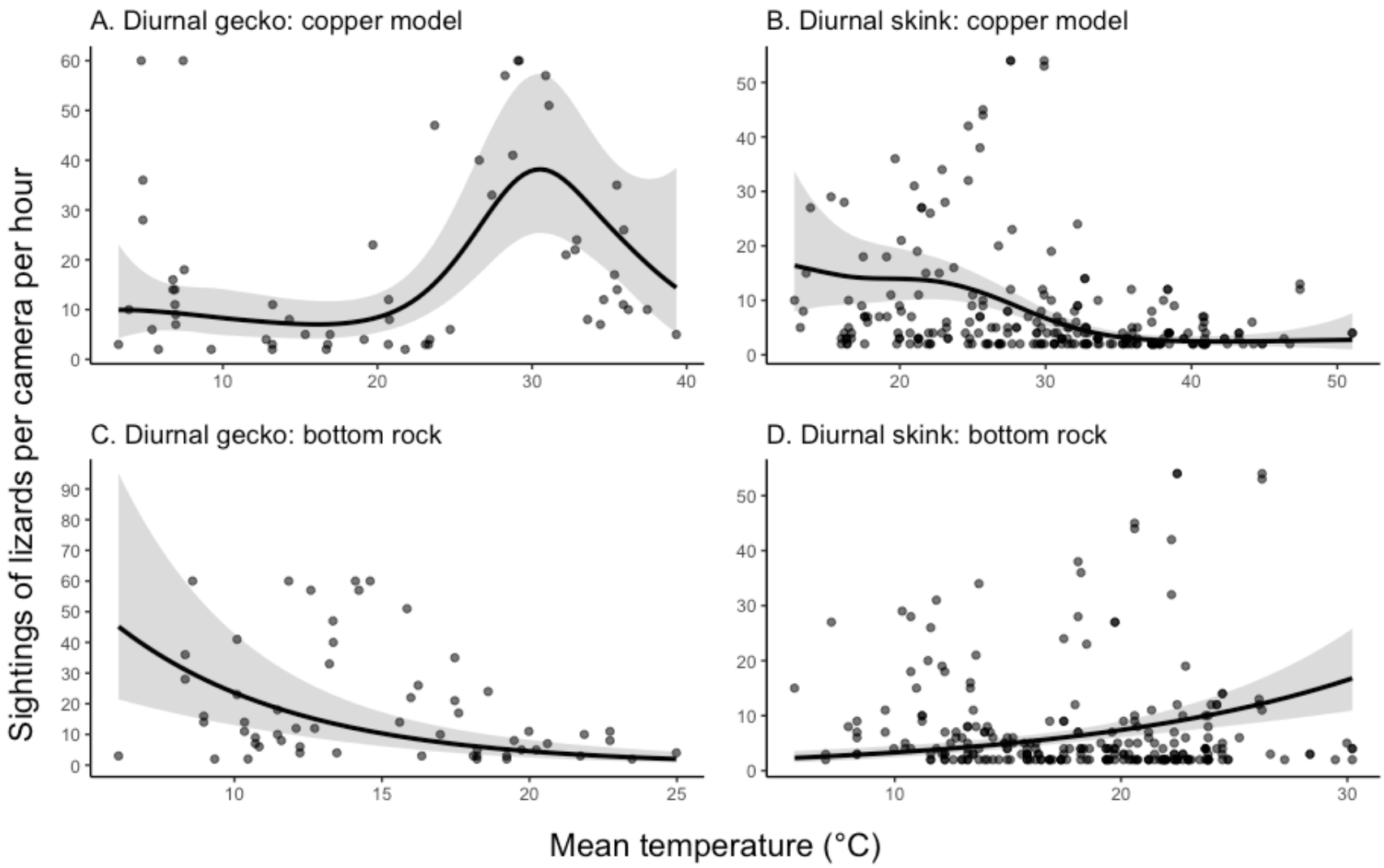

Figure 3.3 Relationships between lizard sightings by day and mean temperature of likely gecko microhabitats in the QL-A site. A is the between diurnal activity of geckos in relation to copper model temepratures which is described by a GAMM. B shows the relationship between diurnal activity of skinks and copper model temperatures as described by a GAMM. C shows the relationship between diurnal activity of geckos and bottom rock temperatures, described by a GLMM. Lastly D shows the relationship between diurnal activity of skinks and bottom rock temperatures as described by a GLMM. Zero values were not included in any models, and the shaded area represents the confidence intervals.

3.3.6 Presence of mammals

I saw evidence of three introduced mammals by night, all of which are potential predators. This includes two photos of a single feral cat (*Felis catus*), three photos of one brushtail possum (*Trichosurus vulpecula),* and one photo of a stoat (*Mustela erminea*). I observed no interaction between these species and lizards on camera.

3.4 Discussion

I observed thousands of nocturnally active orange-spotted geckos from photos taken across the summer season as well as several hundred photos of geckos during the day and thousands of photos of diurnally active skinks. Interestingly, nocturnal activity of geckos was not strongly influenced by the temperature of their microhabitats. At night geckos were present at a wide range of temperatures, including some that were just below 0°C, and were influenced by strong winds. I also observed multiple instances of diurnal surface activity of geckos. Sightings of diurnal surface activity were positively influenced by mean copper model temperatures but negatively influenced by mean bottom rock temperatures (albeit only slightly). Concerning the *Oligosoma* skinks, no nocturnal skink activity was detected. Sightings of skinks were the highest when mean temperatures at copper models were warm, and skink observations increased as mean bottom rock temperatures rose. Diurnal lizard activity was similarly influenced by weather in that fewer individuals were active in the presence of strong winds, rain, and snow. However, sightings of geckos were negatively influenced by wind presence while wind had no affect on skink observations. Lastly, I observed a possum, cat, and stoat. However, I found no evidence of these pests interacting with geckos or skinks.

3.4.1 Nocturnal surface activity of the orange-spotted gecko

It is exceptionally interesting that a single orange-spotted gecko chose to be active when mean environmental temperatures were below 0°C as that is lower than the critical thermal minimum (CT_{min}) for the vast majority of lizards for which it has been evaluated. CT_{min} is the temperature at which an ectotherm loses key functions like locomotion, the ability to gain

nutrition or maintain basal metabolism (Bennett et al. 2018). Studies of CT_{min} on korero geckos (*Woodworthia* 'Otago/Southland') show that the mean value for CT_{min} was ≤1.2°C and that some individuals were able to right themselves when temperatures dropped below that level (Besson and Cree 2011). In international examples, Sunday et al. (2010) compiled the CT_{min} of 128 reptiles and found the lowest recorded CT_{min} to be 1.9°C found in *Leiolopisma guichenoti*. Grigg and Buckley (2013) assembled a similar collection of studies on CT_{min} temperatures from lizards across the world. Temperature data for 158 species were found with the lowest recorded CT_{min} of 2.67°C found in *Liolaemus nigroviridis*. Unfortunately, I do not know the exact body temperature of the individual orange-spotted gecko when it was on the surface. However, in my study, it was active on the surface for two hours in total and in a position where it was partially exposed. As a result, it is reasonable to speculate that its body temperature was between the copper model and the mean bottom rock temperatures at the time (i.e. between -0.8°C and 6.1°C). As a result, it is possible that this orange-spotted gecko may have a CT_{min} that is lower than any species previously included in the global review by Sunday et al. (2010) and Grigg and Buckley (2013). At the very least, this individual will have had a body temperature that is among the lowest recorded for an emerged squamate anywhere in the world.

3.4.2 Diurnal surface activity of the orange-spotted geckos

Throughout the 2018/19 field season, I captured multiple photos of orange-spotted geckos openly basking during the day. This supports other observations of nocturnal New Zealand geckos including *Dactylocnemis* 'Poor Knights', *Hoplodactylus duvauceli,* and *Woodworthia* 'Otago/Southland' all engaging in diurnal activity even though these species are considered to be nocturnal (Jewell 2008; Romijn et al. 2013; Gibson et al. 2015, Jo Monks pers. comm.). In general, diurnal activity of orange-spotted geckos closely matched observations of basking in the Otago/Southland gecko at Macraes in that geckos were observed to bask in short bursts with many body repositions (Gibson et al. 2015). Orange-spotted geckos also often partook in half to full-abdomen basking, a behaviour that was common in pregnant *Woodworthia* 'Otago/Southland' geckos at Macraes(Gibson et al. 2015), but due to the quality of my photos, it was hard to tell whether they were pregnant females or not. Diurnal activity

gives geckos access to warmer day time temperatures, allowing them to reach higher body temperatures. Higher body temperatures increase their ability to move, speed up embryonic development, and promote digestion which ultimately increases the geckos' chances of survival and reproduction (Angilletta 2009; Cree and Hare 2016b; Cree and Hare 2016a). Thus, there are large incentives for orange-spotted geckos to raise their body temperatures by basking during the day.

When orange-spotted geckos were present, their surface activity was strongly influenced by copper model and bottom rock temperatures. The geckos were more active when temperatures at bottom rock positions ranged from 5-15°C and when copper model locations reached between 25°C and 35°C. These temperature ranges likely overlap in time as bottom rocks take longer to heat up and do not reach the same extremes as copper models. This relationship between activity and microhabitat temperatures is very similar to trends that were observed in Chapter 2 and to other New Zealand geckos. Based on spot body temperature work (Chapter 2) I demonstrated that skin temperature of orange-spotted geckos peaks at around 30°C, whereas rock temperature surpassed 50°C (Chapter 2). I observed the same relationship in data from trail cameras when sightings of geckos dropped when temperatures at the copper models surpassed 30°C. These observations are consistent with the preferred body temperature of the korero gecko at Macraes. Korero geckos prefer temperatures of 22-28°C based on thermal gradient research and reach field body temperatures of 15-32°C during the day (Rock et al. 2000; Rock et al. 2002; Cree and Hare 2010). Consequently, I suggest that diurnal activity of orange-spotted geckos follows similar trends to other cool-climate geckos from New Zealand. I only include New Zealand geckos in these comparisons as I could not find an international example of diurnal activity in a nocturnally classified species.

One difference in the diurnal surface behaviour between korero geckos and orange-spotted geckos was their basking duration. Some pregnant korero geckos have been shown to bask for long periods. For example, a single individual was recorded basking for 5.5 h (Gibson et al. 2015). This is much longer than the maximum amount of time that an orange-spotted gecko present on camera in my study, which was just 84 min. A possible explanation is the sex or pregnancy status of the gecko. The korero gecko that was observed for over 5 hours was a

pregnant female. Female korero geckos have higher preferred body temperatures, devote more time to basking, and achieve higher body temperatures than males (Rock et al. 2000; Gibson et al. 2015). Additionally, pregnant females have been shown to have a significantly higher preferred body temperatures (up to 5°C) than non-pregnant females (Rock et al. 2000). Lastly, korero geckos maintain higher body temperatures in early pregnancy (2 months) when compared to late pregnancy (6 months) presumably because less warmth is needed near the end of pregnancy as most of the embryonic development has already taken place (Gibson et al. 2015; Hare et al. 2016). If the orange-spotted geckos that were basking during the day in my study were male or non-reproductive females, it would be expected for them to bask for shorter periods of time than the pregnant korero gecko. Additionally, If the orange-spotted geckos were pregnant females they could be in a later stage of pregnancy when compared to the korero example. This might encourage them to maintain lower body temperatures and thus bask for shorter periods of time.

3.4.3 Diurnal surface activity of *Oligosoma* skinks

Surface activity of skinks followed expected trends, in that activity was highest between mean copper model temperatures of 10-30°C. These temperature ranges are similar to selected temperature (T_{sel}), field body temperatures, and voluntary thermal maximum temperature (VT_{max}) of McCann's skink (*O.maccanni*) in a mid-elevation habitat (Macraes). For example, McCann's skink in early stages of pregnancy selects a mean body temperature of 28.9°C and reaches an average field body temperature of 22.9°C while non-pregnant skinks reach lower body temperature average of 21.5°C (Hare et al. 2009). In a laboratory study of the voluntary thermal maximum (VT_{max}) for the McCann's skink, Virens and Cree (2019) compared the VT_{max} for pregnant females, postpartum females, males, and neonates. The skinks had a mean VT_{max} that ranged between 35.0 ± 0.3°C and 36.0 ± 0.4°C (Virens and Cree 2019). It makes sense for skinks in the alpine zone to prefer these warm temperatures. Environmental temperature and weather generally are expected to play a large role in emergence as they influence the body temperature that individuals are able to obtain, which then potentially impacts an individual's fitness (Cree and Hare 2016b). A popular way to measure this performance is measuring an

individual's sprint speed across a range of body temperatures (Angilletta 2009). In the lab environment, non-pregnant *O. maccanni* follow an expected performance curve, in which sprint speed increases until it reaches an optimal range around 23 to 32°C (Gaby et al. 2011; Cree and Hare 2016a). It is within this optimal range that sightings of skinks reached their peak at my field site. High levels of locomotion, supported by these warm temperatures, could allow skinks to more easily capture prey or hide from predators; thus, it is not surprising that more skinks were active in these periods.

3.4.4 Similarities and differences between lizard taxa and activity periods

Surface behaviour of lizards at my study site varied by species and activity period. Geckos at night had two major types of surface activity. Individuals were either observed leaving or returning to a retreat, or they would remain in the same position for almost an entire night. Diurnal gecko activity was limited as individuals were fairly immobile and skinks were the most active of the two taxonomic groups. These differences could be explained by differences in what they were trying to achieve on the surface. At night the surface activity of geckos probably assists with their nocturnal foraging. Classically, lizards were classified into two foraging techniques. They were considered to be either active foragers, or "sit and wait" predators (Pianka 1966). However, this dichotomy was not apparent in all lizards, and Bauer (2007) suggested that diplodactylid geckos had three foraging techniques. The first is the sit and wait tactic where geckos remain close to crevice entrances waiting for prey to pass by. The second method is slow cruise foraging, where geckos slowly move throughout their habitat continuously looking for prey. The third and final method is serial ambushing, where geckos use several ambushing locations to capture their prey (Bauer 2007; Romijn et al. 2013).

Throughout the night, orange-spotted geckos were observed not moving far from the crevice from which they emerged, but these individuals had a relatively high amount of head movement in which they would look around their nearby habitat. These individuals could be using the sit and wait tactic where the observed head movements could be the individual reacting to nearby prey, although I was unable to see any evidence of prey on the photos. Other observations of geckos at night showed individuals leaving or returning to a crevice which

could be an example of either the slow cruise or multiple ambushing foraging modes. Geckos in New Zealand have been shown to have a wide array of foraging behaviour; for example, the *Woodworthia* 'Otago/Southland' gecko has been observed leaving crevices to forage at night (Cree and Hare 2016b). The forest gecko (*Mokopirirakau* 'Southern North Island') is thought to be a serial ambush forager as individuals moved extensively throughout their foraging period but were often stationary when located (Romijn et al. 2013). Other species such as Duvaucel's (*Hoplodactylus duvaucelii*) and the Poor Knights gecko (*Dactylocnemis* 'Poor Knights') have been observed actively foraging for fruit and nectar from flowering plants (although this is most likely seasonal behaviour; Whitaker 1987). It is possible that the orange-spotted gecko partakes in multiple forms of foraging behaviour, which would describe the observed nocturnal activity. However, it is only assumed that this species forages at night, and to my knowledge, this has not been confirmed. As a result, there is room for future studies look into this issue and further increase our understanding of the activity periods of orange-spotted geckos.

Diurnal emergence in geckos could be a behavioural adaptation made to increase basking or thermoregulatory opportunities. Individuals would expose themselves when there were high thermal incentives to be at the surface. Throughout the basking period gecko movement between open basking positions and the cover of nearby surface rocks is likely thermoregulatory in nature, where the basking individual heats up in the sun and then returns to its retreat to avoid overheating and minimize predation risk (Gibson 2015). Increased levels of active thermoregulation come with inherent costs, such as an increase in predation or a reduction in foraging opportunities as the individual puts its time and effort into thermoregulating (Herczeg et al. 2008). For squamates living in cold environments, investment in thermoregulation is likely to have higher benefits than its associated costs (Row and Blouin-Demers 2006; Besson and Cree 2010; Aguado and Braña 2014). Cold body temperatures limit multiple physiological processes involving metabolism, locomotion and reproduction, limiting the ability of squamates to escape predators, reproduce and develop (Christian et al. 2016). As a result, thermoregulation has been shown to drive lizard behaviour especially in cool or low-quality thermal environments (Gvoždík 2002; Herczeg et al. 2003; Basson et al. 2017). This need

to thermoregulate could be the driving force behind diurnal emergence in orange-spotted geckos.

Diurnal skink activity is similar to diurnal gecko activity in that it is heavily impacted by microhabitat temperature, and both types of lizards were active between 20 and 30°C. The difference is in the amount of movement, as skinks were very mobile during daytime observations. Skinks that are present in tussock-covered scree and boulder habitat are heliothermic ectotherms so it is not surprising that their presence is influenced by warm temperatures and fine weather (Freeman 1997; Holmes and Cree 2006; Lettink et al. 2010) Additionally, skinks that are found in the QLA habitat are considered to be diurnal, generalist foragers that feeds on a large variety of arthropods (Lettink et al. 2010). As a result, skinks were not only present on the surface to bask, but they also needed to forage. As mentioned earlier thermoregulation is often considered the driving factor behind lizard behaviour in low-quality thermal habitat. However, skinks were only active in the QLA habitat when temperatures were warm, conditions were dry, and the sun was at least partially present. As a result, the behaviour observed could be more indicative of skink activity under ideal conditions. When temperatures are favourable lizards have been shown to thermoregulate less precisely and spend time on other activities including foraging, or exploring their environment (Basson et al. 2017). This could explain the difference in activity where geckos were on the surface to bask, skinks were likely on the surface to fulfil a wider array of biological needs resulting in the difference in observed surface behaviour.

Lastly, observations of geckos decreased when wind levels rose. However, observations of skinks were not significantly influenced by wind. The effects of wind on lizards are poorly understood. From the few studies that do exist, the general understanding is that lizards avoid wind as it lowers their body temperature. This happens through the direct cooling of the animal but also by the cooling of the substrate, which in turn cools the animal (Cree and Hare 2016a; Ortega et al. 2017). Wind could also increase the threat of desiccation, especially in dry climates, or make the act of finding prey more difficult by increasing movement in the habitat making prey harder to spot (Sun et al. 2001; Logan et al. 2015; Ortega et al. 2017). There is room for more studies on the effect that wind has on New Zealand squamates. Additionally, the

methods used to measure wind in this study should be improved. Wind data were gathered from observations of tussock movement in photos which was fairly subjective. In addition, over 300,000 photos were manually analyzed to generate all weather observations. This creates the possibility of some input error where observers missed slight changes in weather levels due to the sheer amount of time and effort required to process such a large number of photos. To get a more precise understanding of wind levels, some form of anemometer should be used. A device will allow researchers to obtain precise, objective wind measurements that can be compared with presence observations as well as temperature data to get a more accurate idea of how wind levels are affecting lizard presence.

3.4.5 Mammalian predators present in gecko habitat

I saw three different pest species in my alpine field site. Interestingly I saw no evidence of mice or rats. The pests that were seen were in very few numbers (I only saw one possum, one stoat and one cat). Though it is thought that most introduced mammalian predators in New Zealand remain in habitats that are under 1,100 m a.s.l (Patterson and Bell 2009), there is ample evidence that mammalian predators are present in the alpine zone. Stoats have been found in alpine environments and have been shown to prefer alpine grassland over beech forest habitat (Smith et al. 2007). Stoats are also a proven predator of lizards in lowland habitats as both skink and gecko remains have been found in scat and den contents (Dowding et al. 2015). Feral cats can be found in most regions throughout New Zealand including pastureland, sand dunes, tussock, and native forests. These predators can also be found in most elevations from sea level to the high alpine zone (Zachos 2008). Cats commonly eat birds and rodents, but they have also been known to consume lizards when they are available (Murphy et al. 2004). Lastly, possums are common but in low densities in alpine shrubland and are less common but still present in alpine grassland (O'Donnell et al. 2017). Possums are primarily folivores, but they often prefer higher-quality foods, which include invertebrates or fruits (Nugent et al. 2000). Possums are also known to be opportunistic feeders and consume bird eggs from nests, so it is possible that some predation on small lizards occurs (O'Donnell et al. 2017). These predators appeared at sites where geckos were active, but I witnessed no

interaction between the mammalian predators and the geckos. Additionally, predation of lizards by mammalian predators may be opportunistic, which makes it difficult to detect but still a significant mechanism for lizard population declines (Reardon et al. 2012). As a result, the presence of these predators suggests that there is likely some level of predation of these lizards by introduced pests.

Interestingly I did not record any evidence of mice or rats in the orange-spotted gecko habitat. Mice and rats are both found in the alpine zone throughout New Zealand (O'Donnell et al. 2017). These pests are generalist feeders that have been shown to reduce lizard populations via predation and competition for food resources at lower elevations (Newman 1994; Hoare et al. 2007; Reardon et al. 2012). Mice and rat populations irrupt in podocarp-hardwood forests following a large seed fall and their populations have huge fluctuations over time and space (Ruscoe et al. 2004; O'Donnell et al. 2017). Thus, it is possible that my cameras were active at a period in time where rodent populations were low. If I had recorded after a large seed fall event, I may have recorded activity of rodents in orange-spotted gecko habitat.

Through the use of trail cameras, I have increased our understanding of lizards in a high elevation scree, rock and tussock-covered habitat. We can use this information to improve our ability to monitor these species so that we can increase our understanding of how they interact with their environment. For example, we now know that orange-spotted geckos are more active at night when evenings are calm and that lizards will be on the surface in surprisingly low temperatures; however, it is not completely clear how temperature is affecting emergence at night. Future research can focus efforts on calm evenings across a range of temperatures to try and better understand how temperature influences emergence, where geckos are going when they leave the crevice and what individuals are doing when they remain by surface retreats for an entire evening. During the day lizard emergence is highest when basking positions range from 15-35°C and surface activity greatly decreases when it is raining. In addition. I already know that 95% of all gecko captures occurred when ambient temperature ranged from 9.5 and 19.1°C (Chapter 2). With this knowledge we can plan trips to coincide with warm, sunny, and dry weather so that we have better chances of observing the lizards on the surface. With more

successful monitoring trips, we can increase our knowledge of these species and use that information to generate effective management plans in the future.

Chapter 4 General discussion

4.1 Summary of main findings

The purpose of this thesis was to investigate the thermal ecology and emergence behaviour of alpine lizards, especially orange-spotted geckos. To achieve this, this study first examined the nature of the thermal environment in the habitat of orange-spotted geckos and sympatric skinks (*Oligosoma spp*) over an austral summer (October 2018 to March 2019). The daytime skin temperatures of free-roaming geckos were measured and compared with the surface temperature of their occupied rock to understand the relationship between skin and environmental temperatures. A bio-logger was also attached to a free-roaming gecko to monitor its body temperature in real-time. Lastly, trail cameras were used to monitor activity periods of both geckos and skinks to help understand how temperature and other weather variables influence emergence. I also examined this footage to report on the presence of introduced mammals in the alpine environment.

I recorded a wide range of temperatures in the lizard microhabitats (Chapter 2). Temperatures at sun-exposed basking positions (copper model) were the most variable and included the lowest recorded absolute temperature (-6.5°C) and the highest absolute temperature (68.8°C). Surface rocks that created potential gecko retreats (top rock) were the next most variable microhabitat which was followed closely by temperatures of the substrate within the potential retreats (bottom rock). Lastly, deep crevices, locations potentially used in winter that were 20-40 cm deep, were the most stable position of the four microhabitats that I monitored. In general, geckos were caught with daytime skin temperatures that ranged between 20°C and 30°C. Reproductive females (vitellogenic to late pregnant) maintained significantly higher body temperatures than all other adults. For all individuals, gecko skin temperature had a strong positive relationship with the spot temperature of their retreat's top rock. The skin temperature of males and non-reproductive females increased consistently with the temperature of their occupied rock in an almost linear relationship until around 25 °C, above which the relationship flattened out as rock temperature continued to rise. For female

reproductive geckos, skin temperature was higher than retreat top rock temperature when rocks ranged from 10-15°C but skin temperature was lower when the rocks surpassed 30°C.

Mean temperature of exposed copper models simulating lizards in basking positions significantly influenced the presence of geckos at night in that sightings of geckos decreased, albeit only slightly, as copper model temperatures increased. What is more impressive is that geckos were active at a wide range of copper model temperatures from just above -1°C to almost 15°C. Additionally, nocturnal activity of geckos decreased when winds were strong, and was not influenced by presence of rain (Chapter 3). I also found evidence of orange-spotted geckos basking during the day. Sightings of geckos during the day were influenced by temperatures of the copper model, in that sightings of geckos were highest between 20°C and 30°C after which the number of gecko observations decreased as copper model temperatures continued to rise. Lastly, a relationship existed between wind strength and gecko presence, in that gecko sightings decreased as wind strength rose. *Oligosoma* skinks were only active during the day (Chapter 3). For diurnal activity of skinks more sightings occurred when copper model and bottom rock temperatures rose while sightings decreased in the presence of rain and snow.

Orange-spotted geckos and *Oligosoma* skinks at my field site follow similar trends to what is known of New Zealand lizards in lower elevations including those of korero geckos at Macraes. I recorded a mean skin temperature of 21.6 °C for reproductive female orange-spotted geckos and a mean skin temperature of 19.0 °C for males and non-reproductive female orange-spotted geckos. Korero geckos have a recorded mean body temperature of 22.2°C and 24.9°C for reproductive females and 18.4°C and 21.0°C for males and non-reproductive females (Rock and Cree 2000; Rock and Cree 2008). Additionally, reproductive females of the orange-spotted gecko maintain higher body temperatures than other adults (males and non-reproductive females), which is similar to the difference between pregnant geckos and other geckos (males or non-pregnant females) in the korero gecko at a lower, subalpine site. Finally, both species of geckos are active nocturnally and diurnally and there are multiple examples of diurnal basking at both habitats (Gibson et al. 2015). *S*kinks in the alpine zone also followed similar trends to lower-elevation skinks. *Oligosoma* skinks were sighted more often when rock temperatures ranged from 20-30°C and sightings dropped when rock temperatures surpassed

35°C. In lower-elevation habitat at Macraes the VT_{max} of pregnant female McCann's skinks is 35°C (Virens and Cree 2019). It is possible that skinks at the high elevation site have a similar $VT_{max,}$ which would explain the reduction in surface activity when top rocks surpassed 35°C**.**

4.2 Conceptual model

Conservation projects generate interventions to conserve or manage ecosystems and/or species. These projects are always evolving as we learn more about the species or environment that is being managed and as threats change over time (Salafsky et al. 2001; Margoluis et al. 2009). As a result, monitoring and evaluating conservation projects can be difficult as these projects are not always well documented, goals are not always easy to set, and there are not always clear and identifiable conservation outcomes (Salafsky et al. 2002; Margoluis et al. 2009). To help practitioners consider all the different factors that influence a conservation program a conceptual model can be developed. A conceptual model is a tool that visually describes the context of a conservation program and highlights possible threats that are influencing the target conservation species or ecosystem, such as anthropogenic stressors. These models are communication, planning and assessment tools that allow scientists and policy-makers to understand what a conservation program is trying to achieve and how it plans to do so (Ogden et al. 2005; Moore et al. 2006). I have developed a conceptual model (based on the general alpine model from O'Donnell et al. 2017) to outline conservation targets for orange-spotted geckos and their environment (Figure 4.1). In this model, I focus on orange-spotted geckos as they are more threatened (Nationally Vulnerable) than the majority of the skinks found in the same habitat. This conceptual model highlights possible threats, knowledge gaps and management strategies in an attempt to emphasise what is unknown, what may be threating alpine lizards and how we may go about increasing our understanding of these species and their environment.

The conservation goals for alpine lizards, with emphasis on the orange-spotted gecko, revolve around maintaining lizard habitat and ensuring the species' persistence by limiting threats from predators and people (Fig 4.1). These targets coincide with a draft version of DOC's threatened species strategy to enhance populations of threatened species and limit the

pressures on species from a broad range of threats (Department of Conservation 2017). One point of note is that there are no solid lines (which would be used to denote well-understood relationships) in this conceptual model. This is to emphasize how much we don't understand in terms of alpine lizards, threats to their habitat and population, and the drivers of those threats.

This conceptual model identifies possible threats that may limit our ability to achieve these conservation goals. As a result of monitoring this habitat via trail cameras I know that stoats, possums and feral cats are present (Chapter 3) whereas rats and mice are considered likely to be present as they are found in other New Zealand alpine regions (O'Donnell et al. 2017; Weston et al. 2018). This is represented in the model via the bold arrows connecting mammals to my conservation goals. With the exception of possums, these introduced mammals are all known to prey on lizards to some extent; more generalist feeders, like possums, may be impacting the flora of this alpine habitat (Reardon et al. 2012; Byrom et al. 2016). However, the influence that these mammals have over orange-spotted gecko populations is unknown. Predation rates, recruitment rates (of geckos and mammals), abundance, and density estimates of predators are all unknown. The presence of mammalian predators is enough to imply that they are influencing lizards given better understood relationships in lowland environments (e.g. Reardon et al. 2012), but we need to learn more about this relationship to really understand to what extent.

Another poorly understood relationship is between people and alpine geckos. For example, I know that there are trampers very close to my study site (Chapter 1) and within the alpine habitat of orange-spotted geckos more generally; however, their exact impact on the habitat and lizard populations is unknown. Trampers have the ability to degrade habitat as they traverse it. For example, trampers can unintentionally destroy lizard microhabitat as rocks are dislodged along a trail (Hecnar and M'Closkey 1998). However, we do not know the extent to which this type of disturbance influences alpine lizard populations as there are no studies on the subject in New Zealand. Development in the alpine zone also has the potential to destroy habitat and disrupt lizard populations. Recently, development of a new ski lift in the Crown Range was temporarily halted due to the discovery of a large lizard population. If this construction plan goes through at least 50 ha of lizard habitat will be transformed into a ski

field, leading to the displacement of some lizard populations (Nugent, 2019). A ski field would have massive implications for orange-spotted geckos populations, as it would totally destroy large portions of their habitat. Any lizards that remain in the area will also be affected as mown ski runs change the thermal quality of over-wintering habitat for lizards rendering it thermally unsuitable (Sato et al. 2014). However, the exact impact that development has on alpine lizards is unknown and will depend on the scope of the project as well as any mitigation plans that are put in place.

The drivers behind the listed threats are also poorly understood. For example, snow tussock mast seeding events have the ability to increase pest populations in the alpine zone due to the large abundance of food. Wilson et al. (2010) found that during a summer when the tussock flowered profusely, mouse density increased almost tenfold. This in turn has the ability to increase other predator populations, such as stoats that feed on the mice. However, this is the only study that I am aware of, which examines the relationship between alpine vegetation and predator populations. Additional research is needed to examine how increases in mice populations influence other predator and lizard populations. Research on predator population dynamics coincides with the DOC alpine research programme and its goal to better understand the threats to New Zealand alpine fauna and could be a focus in their future investigations (Chapter 1). In regard to tourism and recreation, New Zealand has solidified itself as a prominent country for adventure tourism (Bentley et al. 2001). As a result, the number of visitors to the alpine zone has increased, and will likely continue to do so, especially around hot spots such as ski hills and popular walking tracks (Booth and Cullen 2001). Growth in tourism can generate additional demand for recreational activities in the alpine zone which has the potential to degrade lizard habitat through the development of additional infrastructure and by more visitors to the alpine zone (Booth and Cullen 2001). Lastly, climate change is likely to influence threats to alpine lizards as well as the lizards themselves. Rising temperatures have the ability to limit activity periods of lizards (Sinervo et al. 2010), and increase the elevational range of a wider suite of invasive species which can impact alpine lizard populations, through predation and competition for resources (Christie et al. 2017).

I have identified three management tools that can help conservation practitioners achieve the outcomes outlined in this model. The primary tool is to control pests directly through animal control. Trapping of pests, such as stoats, cats, rats, and possums, has been successful in low elevations across New Zealand (King and Edgar 1977; Newman 1994; Towns et al. 2007). In the alpine zone, large landscape-scale trapping lines have shown to substantially improve the breeding success of rock wrens (*Xenicus gilviventris*; Weston et al. 2018). However, these traplines are difficult to set up and maintain, due to the rugged terrain of alpine areas. As a result, large-scale aerial poisoning to control rats and mice with secondary poisoning on stoats may be a more realistic option (O'Donnell et al. 2017; Rawlence 2019). Most likely, a combination of both tools will be required to combat mammalian predators in the alpine zone. Secondary tools like advocacy can support the control of pests by raising awareness around the threats to alpine species while explaining the need for management practices (Dowding 2006). Advocacy can also help promote the proper planning of human activity within the alpine zone to limit the impact that tourism has on lizards and their habitat.

Research on orange-spotted geckos has just begun. Through my research, we have a better understanding of when lizards are active in their environment in terms of thermoregulatory behaviour, activity periods, and emergence activity (Chapters 2 & 3). We can use this knowledge to develop and test monitoring protocols which will help to address some of these knowledge gaps. As we learn more, we will get greater certainty about threats to orange-spotted geckos, *Oligosoma* skinks and their habitat from which conservation targets can be refined. In the following paragraphs I have outlined a few examples of possible monitoring and management techniques that can be made more successful by incorporating the findings of this thesis.

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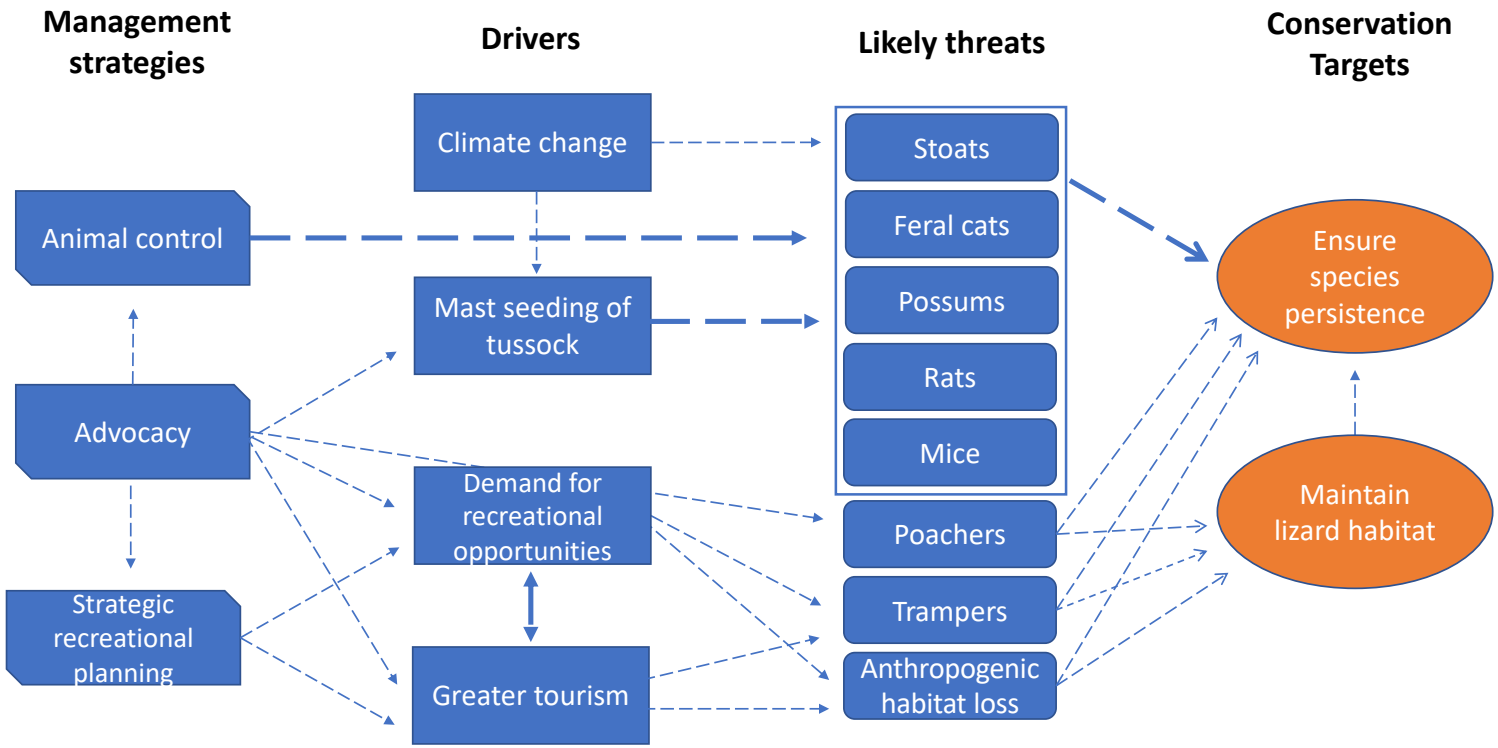

Figure 4.1 Conceptual model for conservation management of orange-spotted geckos. Conservation targets are based on the assumption that orange-spotted gecko populations and habitats are vulnerable. Additional research will tell is if these targets are necessary or if other targets are more important. Likely threats are those that impede achieving the conservation targets. Management strategies can help reduce threats which are generated by the list of drivers. Dotted arrows represent uncertainty between relationships which should be investigated further. Bold dashed lines represent a relationship that has supporting evidence but cannot yet be considered known as parts of the relationship are still poorly understood. The box around some of the likely threats distinguishes threats from predators from anthropogenic threats.

4.3 Monitoring strategies

With information gained through my thesis we have a better idea of when and under what conditions lizards are active in their environment. We can use this information to improve the choice of monitoring tools and monitoring periods to maximise the efficiency of monitoring programs.

4.3.1 Systematic daytime searches

Systematic searches include visual and manual searches of the environment for inactive lizards or signs of lizard activity (Lettink and Hare 2016). These kinds of searches are primarily used to gain information on species presence or monitoring species by obtaining lizard counts and catch-per-unit-effort indices from time-constrained searches (Lettink and Hare 2016). The benefit of systematic searches is that they are inexpensive, easy to repeat, and very successful when conditions are good for finding the target species. They also allow physical contact with the species which enables other forms of assessments to be conducted, including morphometric data collection or palpation to assess female reproductive condition (Wilson and Cree 2003). The disadvantages of systematic searches are that they are labour-intensive, weather dependent, and can be destructive to the habitat (Lettink and Hare 2016; Lettink and Monks 2016).

To improve the quality of the data that are gained through systematic searches the DOC alpine research team has started a photo identification database for orange-spotted geckos. When a gecko is caught a photo is taken of its dorsal markings. These can be used to identify the individual over multiple searches to gather information on survival rates, life-span, and other aspects of population dynamics (Beausoleil et al. 2004). This tool works well for the orange-spotted gecko and *Oligosoma* skink because they have unique markings and the population at my site is within a fairly isolated and well-defined location (Knox et al. 2013; Knox et al. 2019). Internationally that data gained from systematic searches has been used to generate population estimates via site occupancy models (Grillet et al. 2011). For example, 70 random 50 x 50 m plots were established in the habitat of the ocellated lizard (*Timon lepidus*).

Each of the 70 plots was systematically searched and counts of individuals were recorded so that an estimate the lizard population size could be generated. Systematic searches included visual inspection of the site, with binoculars, as well as searches for evidence of the lizard (fecal droppings and tracks; Grillet et al. 2011). These methods could be trialled at my field site. The primary issue is that ocellated lizards are diurnal, which makes them more likely to spot in the open during the day. Daytime searches via binoculars may work for skinks, but not for geckos as they are rarely found out in the open and usually take refuge under surface rocks during the day. As a result, the methods would have to be adapted to include rock turning in order to obtain counts of geckos during systematic searches.

Through my research, we have a better idea of the ideal time to conduct systematic searches. We now know that some geckos and skinks will be active at the surface when mean temperatures at the copper models range from 20-30°C and 95% of all captured geckos were found when air temperature ranged from 9.5 to 19.1°C (Chapters 2 and 3). Sunny, dry weather with light wind may also increase the chances of finding lizards via rock turning. If we organise searches around weather that fits these criteria, then we can improve their effectiveness and gather more information on the orange-spotted geckos. The major issue with long-term monitoring via systematic searches is the disruption that it causes to the habitat. The orange-spotted gecko habitat consists of steep scree slopes with loose rocks and rocky bluffs (Knox et al. 2019). This environment is quite fragile and prone to slips. As a result, systematic searches over a long period of time are likely to have negative impacts on the study site through the actual lifting of the rocks and as searchers move throughout the site. Steps can be taken to limit the impact that searchers have on the habitat such as avoiding loose rocks, using similar walking routes, and taking care to return rock so to the exact position in which they were found (Chapter 2 ; Foster 2012). However, it is impossible to avoid some impact while conducting a systematic search. As a result, we need to be cautious about using systematic searches. They have the ability to reliably gather data and could be used as a means to an end, but they should not be the main tool of a long-term monitoring program.

4.3.2 Tracking tunnels

To limit the impact that researchers have on the study site some monitoring techniques leave devices in the field to monitor lizards remotely (not necessarily in real time). One such tool that could be especially useful in the orange-spotted gecko habitat is the tracking tunnel. Tracking tunnels acquire footprints by coaxing animals, through the use of a suitable bait, across a pre-inked card or inked tray that lines the floor of the tunnel (van Winkel 2008; Jarvie and Monks 2014). Footprints from the animal that are left in the ink can then identify the animal to the genus or species level (Lettink and Hare 2016). In New Zealand, tracking tunnels are typically used to monitor small mammals but they are starting to be used to monitor native species as well, like the giant wētā (*Deinacrida mahoenui*; King and Edgar 1977; Watts et al. 2008). More recently tracking tunnels have been used to identify lizards to the species level by measuring the size of the toe prints, and the toe to sole ratio of the lizard (Jarvie and Monks 2014). Tracking tunnels have already been tested on orange-spotted geckos but in only one instance. Geckos were detected in 5 out of 45 tracking tunnels when they were trialled for a one-month period in April 2016 (Knox et al. 2019). More testing is needed to see if tracking tunnels will be a successful tool in monitoring orange-spotted geckos.

The benefits of using tracking tunnels are that they are less destructive when compared to systematic searches, and they pose no risk to mortality (unlike pitfall traps, which can lead to unintended predation of the caught lizard; Lettink and Cree 2006). This means that tracking tunnels can be left in the field until the ink dries (up to 2 wk) which is especially attractive for use in remote habitats as the tunnels allow for examiners to be in the field for shorter periods of time (Lettink and Monks 2016). The drawback of this tool is that the placement of the traps can influence capture rates, possibly generating a bias in the data that are collected (Lettink and Seddon 2009). In addition, species identification is not always possible (it depends on the quality of the track), and individual identification is impossible (Jarvie and Monks 2014; Lettink and Monks 2016).

In New Zealand, tracking tunnels have been used to develop indices of abundance for cave and ground wētā (*Orthoptera*) in southern beech forest. Wētā footprints on the cards were converted to tracking rate for the whole grid of tunnels, which was then considered to be

an index of abundance (Carpenter et al. 2016). Indices of abundance are useful because they are easier and cheaper to calculate than actual animal density, but they need high detection rates and low variability in order to be reliable (Carpenter et al. 2016). Additionally, indices should be verified against robust population estimates to make sure that they are representative of the target population (Caughley 1977; Carpenter et al. 2016).

Indices of abundance generated through tracking tunnels could be a useful way to monitor orange-spotted geckos and *Oligosoma* skinks in an alpine environment. Through my research, we have an idea of the time of day and temperature range that promotes the activity of these lizards. If we are able to put tunnels out during optimal weather windows, we may be able to detect geckos at a rate that is high enough to generate a reliable index. However, there is currently no robust population estimate for orange-spotted geckos or any of the *Oligosoma* skinks at my field site. When individual identification is possible, photo-identification is a tool that is commonly used in mark-recapture studies to estimate abundance estimates (Wanger et al. 2008; Sreekar et al. 2013). As mentioned earlier, photo identification has already been implemented on orange-spotted geckos and has been used to identify individuals of other New Zealand geckos and skinks (Barr 2009; Reardon et al. 2012; Knox et al. 2013; Knox et al. 2019). Via systematic searches, we could calculate an estimate of abundance through a mark-recapture survey which could generate a reliable abundance estimate. From that estimate, we could validate the indices generated by the tracking tunnels. If the tunnels are able to generate a reliable index, then we would have a repeatable monitoring method that generates a reliable index of abundance. Tracking tunnels could then replace systematic searches as a less disruptive long-term monitoring tool.

4.3.3 Camera monitoring

Another way that we could monitor orange-spotted geckos is via trail cameras. In Chapter 3, I showed that camera traps can be easily set up and left in the field to record activity of geckos and skinks. In my project, trail camera data were used to learn about activity periods, but they could also be used to estimate abundance. There are several examples of trail cameras being used to estimate abundance in large mammals. In these studies, trail cameras were used in mark-recapture analysis to monitor animals with individual identifiable characteristics

(Karanth et al. 2006; Soisalo and Cavalcanti 2006). This is potentially possible to do with orange-spotted geckos and skinks if the photos are of high-enough quality and individuals are close enough to the camera so that their markings can be seen.

A possible solution to this problem is a newly developed herpetofauna-specific camera monitoring system called the Hobbs Active Light Trigger or HALT. This system is a pre-aligned near infrared (NIR) beam which is mounted above and parallel to a sloped elevated platform. The trail camera is triggered when a species walks across the platform and breaks the infrared beam. The slope of the elevated platform is designed to stop debris from remaining on the platform and obstructing the near infra-red beam (Hobbs and Brehme 2017). This system can be designed so that cameras are mounted above the HALT triggering mechanism allowing for dorsal photos of the target species. The HALT system was shown to significantly increase photos of the target species when compared to an unmodified PIR sensor that most trail cameras use (Hobbs and Brehme 2017). The benefits of the HALT system are that it passively monitors the environment and is triggered by lizard activity. This should reduce the total number of photos taken when compared to time-lapse cameras, and the photos that are taken would mostly contain the target species or other species of interest (such as invasive mammalian predators). As a result, the HALT system can be more cost-and time-effective as less time is needed to analyze photos, when compared to a time-lapse camera. The ability to take dorsal photos means that the HALT system could be used to identify individual lizards, which could be used in mark-recapture analysis. However, this system has not been tested in an alpine environment, and the ability to set up the system properly may be limited by access to flat, sheltered areas. Additionally, the system requires a lizard to move across it in order to break the NIR beam and trigger the camera, which may be difficult to achieve with lizards in the alpine environment.

Alternatively, new methods using trail cameras have been able to generate abundance estimates where individual identification is not necessary. A method that might work on orange-spotted geckos is an instantaneous sampling model. This approach treats photos taken by time-lapse cameras as replicates of spatially and temporally fixed area counts (Moeller 2017; Moeller et al. 2018). As a result, the number of animals in a single picture is a sample of density

at a point in time in the camera's frame. When an array of cameras is deployed to randomly selected areas, each photo represents an instantaneous snapshot of the overall density in the study area. As cameras take additional photos over time, further temporal replicates of density estimates are generated. Estimates of abundance can then be extrapolated from these density observations (Moeller 2017; Moeller et al. 2018). I have already used time-lapse cameras to monitor orange-spotted geckos with some success (Chapter 3). In addition, orange-spotted gecko habitat is relatively secluded and remote so that people have a low chance of disrupting the camera grid. The main problem with this technique is that it was originally tested on elk (*Cervus canadensis*), a large, easily identifiable, mammal. Orange-spotted geckos, on the other hand, are small, cryptic ectotherms. Lower detection rates or the influence of temperature or weather on emergence may impact the ability to generate abundance estimates on orange-spotted geckos through instantaneous sampling (Hitchmough et al. 2016; Knox et al. 2019). With that being said, instantaneous sampling is a novel technique that may be a low-impact way to monitor geckos and increase our understanding of their population levels. Camera monitoring can be run in tandem with tracking tunnels to generate multiple estimates of abundance and comparing the results from each method should give us a better idea of the true population size of orange-spotted geckos.

4.3.4 Monitoring predators

My research has confirmed that introduced mammalian predators (including possums, stoats, and cats) are present in the habitat of lizards at the QL-A site. However, we do not know the density or the true number of species that are present nor do we know how they are affecting the orange-spotted geckos or *Oligosoma* skinks. As a result, there is a need to increase our understanding of the abundance of predator populations, and the predator-prey dynamics between mammalian predators and the orange-spotted gecko. Many of the tools that I have suggested we use to monitor lizards can also be used to monitor introduced mammalian predators. Tracking tunnels have been to monitor small mammals, like stoats, and to generate rodent-density indices (Blackwell et al. 2002; Morgan et al. 2009). However, monitoring mammals with tracking tunnels can be difficult. Smith and Weston (2017) for example, found that a well-established tracking tunnel index was unable to detect stoats in an alpine

environment, even though their presence was recorded via remote trail cameras. Trail cameras have also been used to monitor predator presence as well as to estimate the relative abundance of predator species like the feral cat, stoat, and hedgehog (Glen et al. 2013; Glen et al. 2014; Glen et al. 2016). We could also conduct gut content analysis to see what role geckos and skinks play in the diet of these introduced predators (Jones et al. 2005; Murphy et al. 2005; Murphy et al. 2008). Alternatively, DNA analysis of scat can also be used to determine the diet of predators (Klare et al. 2011). There is a wide array of tools that are available to help us better understand how many predators reside within this alpine lizard habitat. None of these tools are 100% effective, and it will likely take a combination of methods to give us a strong understanding of the presence of predators at my field site.

4.3.5 Anthropogenic threats

Lastly, there is the possibility of human interference with orange-spotted geckos and skinks at my study site. A popular walking track also used by mountain-bikers goes directly through lizard habitat where geckos are known to be. Due to the potential poaching risk, the existence of geckos along this track has not been disclosed to the public. As a result, when trampers go off trail they will unknowingly trudge through orange-spotted gecko habitat and have the ability to crush or disrupt lizards. This poses an interesting dilemma. At the same time as the presence of orange-spotted geckos is being kept a secret as protection from poachers, this secrecy is increasing the risk of accidental death at the feet of uninformed trampers. At this point in time we do not know the extent to which either of these threats occurs. In Point Pelee National Park, Canada high-traffic areas become degraded and lose microhabitats, like small woody debris, that are preferred by native skinks (*Eumeces fasciatus*). This results in a decrease of lizard abundance where tourists are more active (Hecnar and M'Closkey 1998). Without proper replacement movements of rocks can cause negative effects on lizard populations. Improperly replaced rocks turned during systematic searches have been shown to harbor fewer lizards and maintain lower temperatures than undisturbed rocks (Pike et al. 2010). As a result, it is not farfetched to suggest that trampers are negatively impacting lizard habitat that they travel through.

A possible solution to this problem is to encourage trampers to stay on the marked trail. This would reduce the chance that trampers will inadvertently crush geckos under surface rocks and could be done while keeping the presence of the geckos a secret. Signage at the start and throughout trails has been shown to encourage positive behaviour in trampers (Hockett et al. 2017). However, personal communication, where trampers receive an oral explanation about how their behaviour can affect the environment, is considered to be the most effective way to generate desired behaviour from visitors (Widner 1998; Widner and Roggenbuck 2003). Ultimately a combination of these tools could help protect geckos from off-trail trampers (Hockett et al. 2017). Signs could be installed at the beginning and throughout the marked trail, and staff at information centres can encourage visitors to stay on trail to conserve the alpine environment in New Zealand. Hopefully, this message will cause a change in behaviour where trampers stick to trails and limit their impact on alpine gecko habitat.

Alpine lizards in general, and the orange-spotted gecko in particular, are fascinating species living in an extreme environment. These alpine species, as well as all life on earth, face a significant threat in the form of climate change. New Zealand has already begun to see the effects of climate change through temperature increases, warmer, winters, decreased frost frequency, retreating snowlines, and rising sea levels (Christie 2014). New Zealand is expected to have increased temperatures; best estimates state a mean increase of 1°C by 2040 and 3°C by 2090 (Ministry for the Environment 2016). Precipitation is expected to vary on east-west and north-south gradients. As a result, the west of the North island and the south west of the South Island is expected to have more rainfall, especially in winter. Conversely, the north and east is expected to have less rain, meaning more dry periods in coastal Canterbury and coastal Marlborough on the South Island (Christie 2014).

Rising temperatures are expected to make many lizard species reach their voluntary thermal maximum more frequently. In response, lizards will have to spend more time taking refuge from the heat, which reduces their ability to partake in other activities, like foraging (Sinervo et al. 2010). Additionally, increasing temperatures are expected to cause many species to move higher in elevation in search of cooler temperatures. This further impacts alpine species as their habitable space shrinks and becomes inundated with other species (Wilson et

al. 2005). This could potentially create more competition for habitat and resources as lower-elevation lizards shift upwards towards orange-spotted gecko habitat. Shifts in range will also occur for predator and pest species. Temperature shifts are likely to make the alpine zone suitable to a broader range of pests and predators for a longer period of time (Gilman et al. 2010). As a result, alpine lizards, including the orange-spotted gecko, may face an increase in predation risk in addition to more competition for food resources. Elevational shifts upwards by both native and introduced animals may require increased management interventions. Additional trapping efforts in the alpine zone may be required to cope with predators that are able to remain in higher elevation zones for longer periods of time. Additionally, translocations may be required as native species begin to compete for suitable habitat. The more we learn about these possible scenarios the better we can deal with changes to our environment that are generated by climate change. With effective monitoring programs, we will be able to improve our knowledge base and do our best to promote the long-term stability of alpine lizard populations and the remote alpine environment in which they live.

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Appendix 1

1.1 Thermal preference

In ectotherms, environmental temperature influences body temperature, which in turn, effects physiological processes of the individual (Angilletta 2009). Extremely low or high body temperatures are harmful or even lethal to ectotherms, whereas more moderate to high body temperatures often maximise functional abilities (Qu et al. 2011). As a result, ectotherms attempt to maintain relatively high and constant body temperatures or temperatures that are within their preferred body temperature (PBT) range (Qu et al. 2011). PBT or selected temperature (T_{sel}) are the temperatures selected by individuals in absence of constraints for thermoregulation (Camacho and Rusch 2017). Thermal preference of lizards is often measured on a thermal gradient. A thermal gradient is a joined compartment that offers an organism the ability to choose its temperature, usually through the heating of the compartment's surface across a range of temperatures (Angilletta 2009). By placing a lizard in an environment where only temperature varies, we can understand what body temperature it would prefer to be in ideal circumstances (Angilletta 2009). Thermal preference provides information on thermoregulatory strategies in environments where no ecological constraints exist. Combining this information with measurements of body temperatures in natural environments, we can see whether individuals regulate their body temperature in an environment where many factors can influence their behaviour (Angilletta 2009).

Usually, individuals are placed on gradients from anywhere between 7 to 24 hours, to give the lizard time to relax and settle on its preferred temperature (Lailvaux et al. 2003; Hammer et al. 2018). As a result, studies that use thermal gradients often take place in the laboratory where there is access to electricity to support the long period of time that lizards are left on the gradient (Le Galliard et al. 2003). As a part of my thesis I attempted to develop and test a portable thermal gradient that would allow researchers to test the preferred body temperature of individuals in the field. This device can be

easily assembled and runs off a 12V vehicle battery. The major benefit of this device is that lizards do not need to be removed far from their habitat to test their preferred body temperature. Instead the gradient is brought close to them. This device was developed as I did not have a permit to remove orange-spotted geckos from my field site. Even if I did, it would be a difficult operation as the site is fairly remote and access is limited. As a result, a fully functional portable thermal gradient would allow us to discern the T_{sel} of this remote alpine species and could be used in other studies with similar access restrictions.

1.2 Thermal gradient

The thermal gradient was designed by Stu Borland, a technician in the Department of Zoology at the University of Otago. Stu dedicated a significant amount of time and energy to make the device portable and able to run with a limited power supply. Without his help testing this gradient would not have been possible.

The gradient is an acrylic compartment that is 760 mm long x 80 mm wide x 120 mm high. The substrate of the gradient consists of ceramic tiles, which are heated by a series of Peltier devices powered by a 12V battery. These devices are programmed to heat to a specific temperature, which is controlled by a thermistor and an Arduino microcomputer. I aimed for the gradient to generate surface temperatures from ambient (~10°C) to a maximum of 36°C, which is above the maximum temperature that geckos are expected to select (Rock et al. 2000). The gradient then has an acrylic insert that gives the gecko something to press up against and the entire gradient was darkened, by covering it with a black cloth cover, to simulate being in a natural retreat (Fig A.1). A bio-logger (Chapter 2) was be attached to the individual in the gradient so that the body temperature of the individual could be measured for the duration of the experiment. Examinations were limited to the late morning and afternoon, when thermal preference is likely to be high (Rock et al. 2000). Each individual was placed in the gradient for 2-3 hours. This time duration is much shorter than other studies where individuals are kept in a gradient for 24 hours up to two days (Rock et al. 2000; Preest and Cree 2008). However, a shorter examination was necessary because the portable gradient has a limited power supply

which makes a 24-hour test not possible. Using this gradient, I hoped to compare the selected body temperatures for both pregnant and non-pregnant geckos in summer and in autumn.

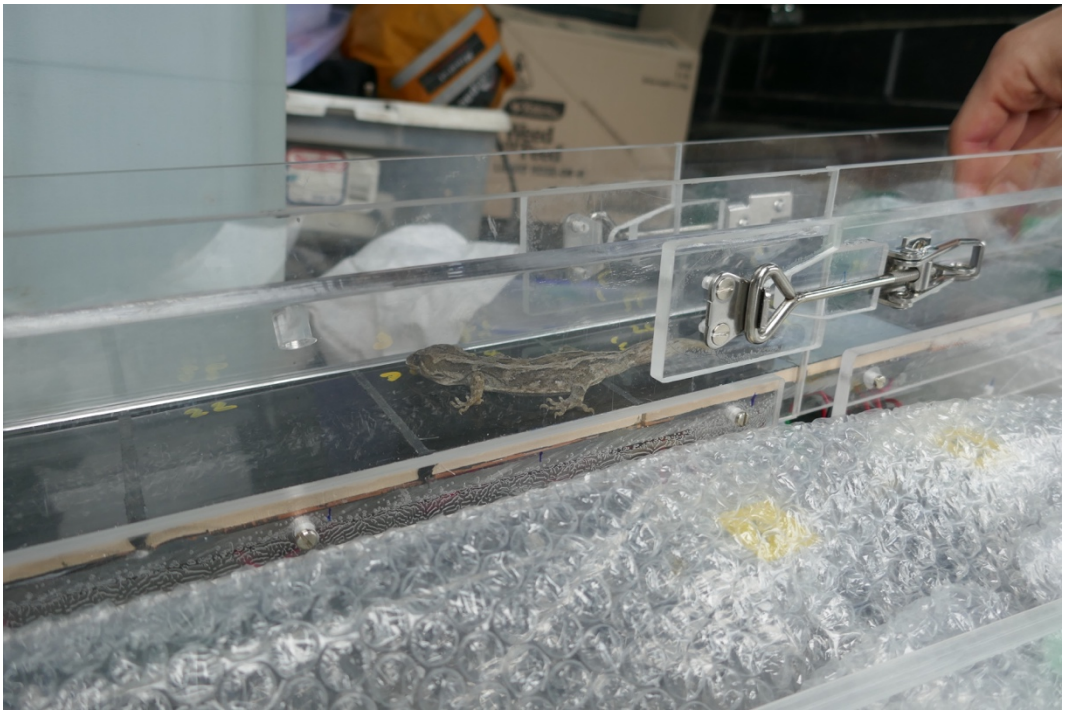

Figure A.1 Photograph of the thermal gradient with an orange-spotted gecko inside. The photo was taken before the gradient lid was put on and before the gradient was covered with a dark cloth. Each black tile was programmed to reach a different temperature to generate the gradient.

1.1.1 Attempt 1

First, I ran the gradient outside on the ground near our field camp. I placed the gradient in a small tent to create shelter from the wind to try and limit the impact that the sun had on the tiles. The gradient had no ability to cool the tiles that make up its surface. As a result, the lowest temperature on the gradient was similar to ambient temperature and the rest of the gradient was created by incrementally heating up the remaining tiles. As a result, the sun or other weather variables have a large impact the gradient. I hoped that the tent and the black sheet over the gradient would be enough to limit the impact that external heat sources had on the device. Unfortunately, it did not. The sun and warm weather heated up the entire tent causing all of the tiles on the gradient to reach temperatures in excess of 30°C. Waiting for days

with cool weather was not a practical solution so I tried to find a better way to shelter the gradient from the elements.

1.1.2 Attempt 2

Next I tried to run the gradient in the back compartment of the truck which was parked at the field camp. This location provided shelter from the sun and more airflow than the tent. Unfortunately, using this location did not solve the problem as the lower end of the gradient was still too warm.

1.1.3 Attempt 3

In my last attempt I tried to run the gradient in the truck with the air conditioning running. The hope was that the inside of the truck would create a cool, protected, environment where the gradient would work as intended. I tested this idea at a lower elevation in the same vehicle in shaded conditions and was able to produce a stable gradient. In my test, I cooled the inside of the truck to 10°C and from there heated up the tiles to form a gradient. Unfortunately, when I repeated this at my field site the gradient did not function properly. This time tiles on the gradient were not acting as programmed. They would heat to temperatures that were higher or lower than what they were programmed for, for unknown reasons. After days of attempting to reprogram the gradient in the field I abandoned the attempt. I suspect a coding or hardware issue was causing these new problems as I had removed the ability of the outside environment to interact with the gradient. It is also likely that the increased amount of solar radiation, and the presence of more variable conditions caused the gradient to fail. I think that it is still important to learn the preferred body temperature of orange-spotted geckos. This information would give us a much better idea how the thermal environment of their alpine habitat is affecting their field body temperatures. It would also allow us to make comparisons with the preferred temperature of other cold adapted ectotherms to see if there are any evolutionary adaptations in the orange-spotted gecko. Lastly the portable thermal gradient would be a great tool to develop so that it can be used on other remote or hard-to-reach species so that we can increase the knowledge base of alpine squamates as a whole.

Appendix 2

2.1 Development of methods for the successful attachment and retrieval of miniaturised bio-loggers from free-roaming orange-spotted geckos

The following methods describe four unsuccessful attempts to attach and retrieve bio-loggers from free-roaming orange-spotted geckos. Information learnt from these failures allowed the generation of one successful bio-logger recapture, which is described in the Chapter 2.

2.1.1 First attempt

My first test of attachment used dummy bio-loggers instead of fully functioning loggers. I used dummy loggers because I only had access to a limited number of functioning loggers, as they are fairly expensive, and wanted to have a better idea of how the attachment would work before I committed real loggers. I attached these dummy loggers to two individuals (J1 and M1) during October 2018. The dummy loggers were old bio-loggers which no longer functioned as they had been damaged during use in a different study. I placed a piece of double-sided Sellotape directly onto the bottom of the dummy logger. I then placed the bio-logger onto the dorsal side of the gecko just above its hindlimbs. Next, a strip of Nexcare Micropore first-aid tape was wrapped over the device to better attach it to the skin. The tape was cut into two small strips that were placed on the top and bottom of the bio-logger. I made sure that the tape did not connect to form a complete ring around the body of the gecko as I considered that this would aid the device to fall off the gecko if I failed to relocate it (Virens and Cree 2018). I also glued UV stickers to the bio-logger. These stickers are highly visible when they are illuminated with a UV torch so I hoped that they would increase our ability to find the bio-logger in the field. Once the dummy loggers were attached, I attempted to relocate the geckos after 2 d. I returned to the locations where the geckos with the attached loggers were released and turned rocks, starting from the rock that I found the gecko under originally slowly moving outwards searching every possible retreat location within a 50 m radius. Additionally, one nighttime search was conducted with a UV torch to increase our chances of seeing the UV stickers. I found no geckos during the nighttime search and was unable to relocate either of the geckos. I also

did not find the loggers on the ground during my search. Interestingly, on the next field trip in November I found one of the dummy loggers in the soil underneath a surface rock within 10 m of the release site.

2.1.2 Second attempt

In November 2018 I tried again, this time with functional bio-loggers. I tried the same attachment as used in October, but I made some changes to try and increase the recapture rate of the bio-loggers. Bio-loggers were attached to four individuals that I found during the day searches. This time I attempted to relocate the geckos after 24 h instead of 2 d. I hoped that the individuals would move less in 24 h, allowing me to find the individual under the rock that I released it to, or in the same general vicinity.

Additionally, I attempted to use UV powder to increase our chances of finding an individual. The UV powder is a non-toxic component in common paints that has a bright UV colour. Once the logger was attached, and the gecko was ready to be released, I dipped the feet of the gecko into the UV powder so that it would leave a trail behind when it moved throughout the site. I hoped that I would be able to relocate this trail which would give us a better idea of where the gecko may be. Lastly, I only mounted bio-loggers on individuals that I found in secluded locations that contained few to no deep crevices and a limited number of retreats in the surrounding area. By limiting the time between attachment and relocation and choosing more secluded locations, I hoped that I would be more able to relocate the individuals. Once again, I returned to the original rock that I found the individual under. I looked under that rock and worked outwards searching every possible gecko retreat. When I was unable to relocate the gecko, I returned the following day searching the area in the same manner. However, I was unable to find a logger on the gecko, in the soil, or under any surface rocks.

2.1.3 Third attempt

For my third attempt I tried to improve our recapture rate by including a VHF device to the attachment at the suggestion of Jo Virens. I used a small Pico Pip radio transmitter weighing a total of 0.25 g (Pico Pip Ag 337 from Biotrack, Dorset, UK). The transmitter was attached directly to the top of the bio-logger with epoxy so that if the bio-logger fell off, I would still be

able to retrieve both devices. I fashioned the transmitter so that the antenna of the device followed the tail of the gecko. The combined VHF transmitter and bio-logger device were attached as on previous trips. However, the combined devices weighed a total of 0.63 g, double the weight of the bio-logger on its own. As a result, I was only able to attach the device to large individuals to remain within the approved limit of ≤5% of body mass. I then attempted to relocate the device after 24 h and only used individuals that I found in secluded locations. With this method I was able to recover one of the three devices. However, the device was no longer attached to the gecko and was instead found in the scree less than 5 m downhill from where I released the gecko. Although I was able to retrieve some temperature data from the bio-logger I am unsure when the device fell off of the individual, which makes it hard to tell if the recorded temperature is gecko body temperature or just ambient temperature.

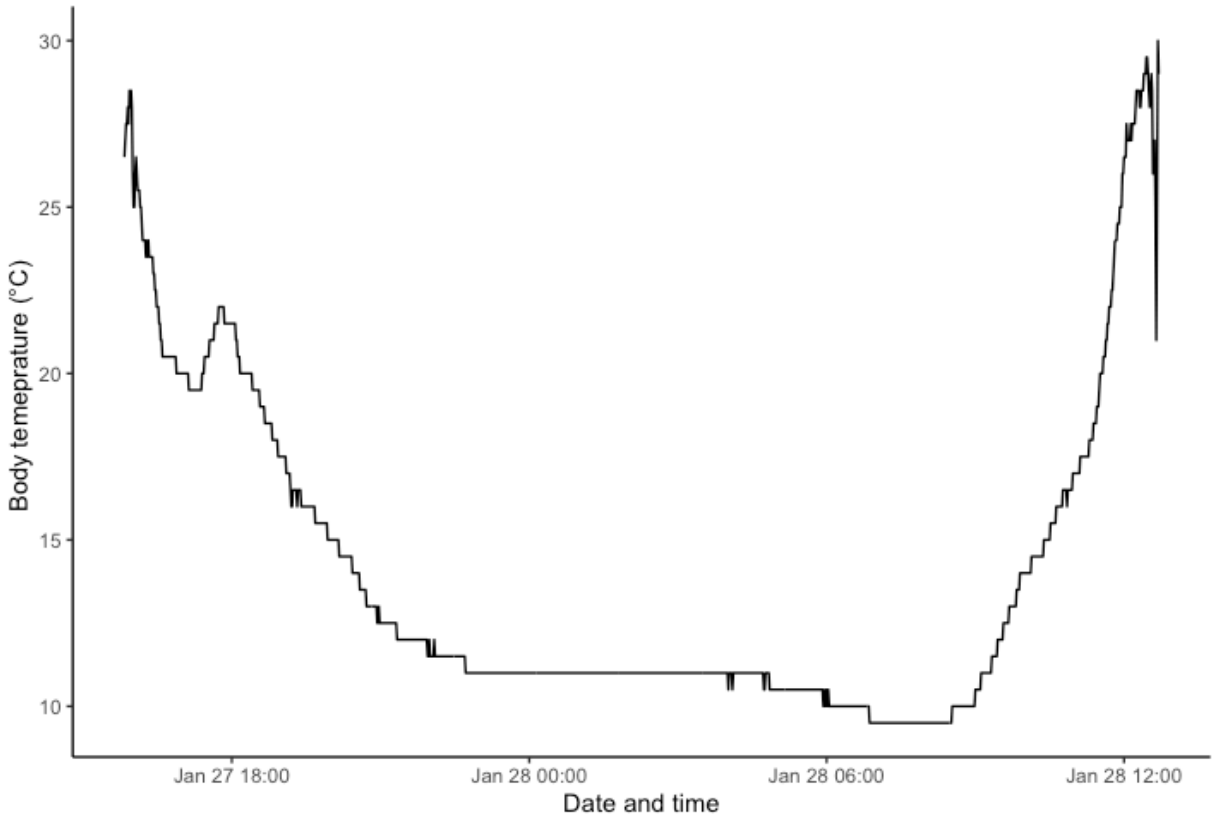

Figure A. 2 Temperature recorded by a miniaturised bio-logger intended to monitor the body temperature of a free roaming orange-spotted gecko over a 24-hour period. This bio-logger was found on the scree less than 5m from where the gecko was released. As a result, we do not know what temperature represents gecko body temperature and which represents ambient environmental temperature,

Appendix 3

These tables are supporting information for Chapter 3. They show the results of GLMM and GAMM that were run to compare emergence activity of geckos and skinks with bottom rock microhabitat temperature and other weather variables namely presence of rain, strength of wind and presence of snow.

Table A.1 Results from the GLMM and GAMM of diurnal gecko presence data comparing sightings of geckos to microhabitat temperatures and weather variables. Significant values are in bold. Weather was not included as a factor as geckos were only present on sunny dry days.

	Diurnal gecko emergence GLMM			Diurnal gecko emergence GAMM		
	DF	**X^2**	**P**	**EDF**	**X^2**	**P**
Temperature of copper model	1	17.911	**< 0.001**	4.397	38.87	**< 0.001**
Temperature of bottom rock	1	30.357	**< 0.001**	1	13.64	**< 0.001**
Wind	1	5.502	**0.019**	1	4.288	**0.038**

Appendix 3

Table A.2 Results from the GLMM and GAMM of nocturnal gecko presence data comparing sightings of geckos to microhabitat temperatures and weather variables. Significant values are in bold

	Nocturnal gecko emergence GLMM			Nocturnal gecko emergence GAMM		
	DF	**X^2**	**P**	**EDF**	**X^2**	**P**
Temperature of copper model	1	2.888	0.089	2.569	10.456	**0.024**
Temperature of bottom rock	1	1.167	0.280	1.634	2.562	0.288
Wind	1	0.249	0.618	1	0.204	0.651
Weather	1	0.008	0.928	1	0.891	0.345

Appendix 3

Table A.3 Results from the GLMM and GAMM of diurnal skink presence data comparing sightings of geckos to microhabitat temperatures and weather variables. Significant values are in bold. Weather was not included as a factor as skinks were only present on sunny dry days.

	Diurnal skink emergence GLMM			Diurnal skink emergence GAMM		
	DF	**X^2**	**P**	**DF**	**X^2**	**P**
Temperature of copper model	1	71.711	**< 0.001**	4.455	83.95	**< 0.001**
Temperature of bottom rock	1	24.588	**< 0.001**	2.742	29.71	**< 0.001**
Wind	1	0.663	0.416	1	0.200	0.655

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